# Understanding the spatiotemporal recruitment dynamics of commercially important fish species in the North Sea

**Dissertation with the aim of achieving a doctoral degree at the**
**Faculty of Mathematics, Informatics and Natural Sciences,**
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# 1 Summary

Nearly 75% of marine fish stocks are overexploited and management based on sound science is needed to promote stock recovery and sustainability. Understanding recruitment, the number of fish entering the fishable stock every year, is key to sustainable management strategies. During the early-life period of fish, rates of natural mortality are extremely high and even small fluctuations in these rates can generate orders-of-magnitude differences in recruitment. For more than a century, fisheries scientists have developed various hypotheses explaining recruitment variability. At the present time, it is widely acknowledged that observed variations in fish recruitment most likely result from a combination of bottom-up and top-down processes acting at various temporal and spatial scales during fish early life. However, the variability in the magnitude of these processes remains largely undocumented and poorly understood leading to competing or sometimes even conflicting hypotheses on recruitment drivers.

This thesis addressed the need for further investigation of the spatial and temporal variability of the processes driving recruitment variability of commercially important fish species in the North Sea. In Chapter 4, a solid basis for analyses of the spatial and temporal variability of North Sea hydrography was produced. A physical-statistical model (Adjusted Hydrography Optimal Interpolation, AHOI) was developed to produce gridded hydrography based on available oceanographic observations. AHOI was mainly based on optimal or Gauss-Markov interpolation and included routines for data quality control such as the removal of outliers and instabilities, and corrections for vertical density stability. This model is general applicable to hydrographic data collected in various regions of the World Ocean. In Chapter 4, the AHOI was applied to produce high-resolution (0.2° x 0.2°) monthly maps of temperature and salinity in the North Sea for the period between 1948 and 2013. These maps were extensively validated using available alternative data products and time-series of observations, excluded from the analyses for the validation purpose. The accuracy of 0.3 °C for temperature and 0.1 for salinity maps was assessed. The AHOI dataset was made freely available for the scientific community to promote its use in ecosystem-related studies.

In Chapter 5, the AHOI maps were used to explore how the environment influences the biomass and reproduction of nine commercially important fish species in the North Sea. The stocks examined were: Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), European plaice (*Pleuronectes platessa*), haddock (*Melanogrammus aeglefinus*), Norway Pout (*Trisopterus esmarkii*), whiting (*Merlangius merlangus*), common sole (*Solea solea*), and saithe (*Pollachius virens*). Five stock variables were analyzed (spawning stock biomass, recruitment,

pre-recruitment survival index, and the log-transformed versions of the last two variables). Spatially-explicit cross-correlation analysis allowed to identify, for the first time, areas of the North Sea where environmental conditions appeared to have stronger or weaker influence on the stock variables. Given the heterogeneity of the North Sea hydrography and various physical processes controlling its temporal variability in different parts of this shelf sea, this information can help to identify processes underlying significant stock-environment correlations. The analysis revealed a positive correlation between water temperature in the north-western North Sea and herring spawning stock biomass, and a negative correlation between temperature in the southern North Sea and the pre-recruitment survival index of sole. A positive correlation was found between water salinity and the spawning stock biomass and recruitment of sprat. Moreover, the results of Chapter 5 confirmed known relationships between recruitment of cod and plaice with water temperature. Plaice recruitment was found to correlate with temperature in the southern North Sea, whereas the strongest correlation between log-transformed cod recruitment and water temperature was found in the north-western North Sea, in the region of the Atlantic Water inflow. These findings pointed out the importance of the Atlantic Inflow for the recruitment dynamics of North Sea cod. The correlation between water temperature and log-transformed cod recruitment was found to be strong (-0.86) and stable over the whole period of observations from 1963 to 2013. A novel statistical method of incorporation of environmental covariates into stock-recruitment models used in fishery management was proposed using an example of North Sea cod.

Starvation and predation during cod early-life stages (ELSs) have been previously suggested to be the main regulators of cod recruitment in the North Sea, whereas only starvation has been considered as a plausible mechanism behind the observed negative correlation between cod recruitment and temperature. Less is known on how temperature may control predation mortality. It was tested in Chapter 6 whether temperature-induced changes in the consumption rate of the main predators on cod ELSs can cause the observed relationships between recruitment and temperature. A biophysical model was developed to study the interplay between temperature-dependent growth and mortality rates of cod ELSs. This model consisted of three coupled components: 3-dimentional hydrodynamic model (HAMSOM), Lagrangian drift model and an individual-based model, simulating growth and mortality of cod eggs, larvae and juveniles. Herring, sprat, adult cod, whiting and grey gurnard (*Eutrigla gurnardus*) were included as predators. The biophysical model was validated using the observed size-distribution of cod juveniles in the North Sea. It was shown that the survival of cod eggs only slightly increased with increased temperature, because the reduction of the cumulative mortality due to faster development at higher temperatures was almost fully compensated by increased predator consumption. Cod larvae were found to survive better at warmer temperatures. The opposite was found for juveniles: they experienced a higher survival if temperature was low. The survival of cod through the entire early-life period was found to increase with increasing temperature. The findings of Chapter 6, even though being obtained only for North Sea cod, contributed to the "growth-survival" paradigm, one of the main hypotheses of the fish early-life stages biology. It was demonstrated that fish early-life stages profit from warmer ambient temperatures only if the ratio between the temperature coefficients for the rate of growth and the rate of predator consumption exceeds 1.

In Chapter 7, the biophysical model was further developed to study other factors controlling the strength of predation mortality of cod ELSs in the North Sea. Next to temperature, the annual changes in the biomass of main predators and changes in their spatial distribution were considered. A spatially-explicit predator consumption was included in the mortality term based on the observed abundance, diet and distribution of the predators listed above. The model results showed that including realistic predation in the biophysical model altered substantially not only the spatial pattern of cod ELS survival but also the mean survival and its temporal variability. The mean survival obtained in the realistic simulation was two orders of magnitude higher than the one obtained in the homogeneous simulation, suggesting that cod ELSs might benefit from a patchy spatial distribution of their main predators in the North Sea. The sensitivity experiments performed in this chapter showed that the variability of the spatiotemporal overlap between cod ELSs and their predators is an important driver of the inter-annual variability of the survival of cod ELSs in the North Sea. Its impact was found to exceed those of the hydrographic variability and the annual changes in predator biomasses.

The results of this thesis advanced our understanding of the processes driving recruitment variability of commercially important fish species in the North Sea, particularly North Sea cod. The tools and concepts developed here are readily transferable to other data-rich systems and stocks. The thesis emphasized that it is essential to understand the spatial dynamics of the processes and factors affecting the survival of fish ELSs in order to understand and ultimately forecast the annual variability in recruitment for management purposes. Developing a biophysical model with realistic predator fields was an important step towards understanding how variability in predation mortality of ELSs may control the stock dynamics of Atlantic cod in the North Sea. The results of this thesis will form a useful contribution to the scientific advice for cod fishery management and marine spatial planning in the North Sea.

# 2 Individual scientific contributions and outline of publications

This outline describes four manuscripts included in this thesis and the individual scientific contribution of each author. Three manuscripts have already been published in peer-review journals, the forth manuscript will be submitted soon. The results of the four studies used in this thesis have been presented at several international conferences, namely: “The Future of Operational Oceanography” (Hamburg, Germany, 2013), „Johan Hjort Symposium on Recruitment Dynamics and Stock Variability” (Bergen, Norway, 2014), “3rd International Symposium: Effects of Climate Change on the World’s Oceans” (Santos, Brazil, 2015), “39th Larval Fish Conference” (Vienna, Austria, 2015), “40th Larval Fish Conference” (Maryland, USA, 2016) and “ICES Annual Science Conference” (Riga, Lithuania, 2016).

## Chapter 4

### Monthly maps of optimally interpolated *in situ* hydrography in the North Sea from 1948 to 2013

Anna Akimova (AA) conceived the idea of the study. Ismael Nunez-Riboni (INR) developed the model and performed the programming. AA conducted the validation of the AHOI maps, contributed to manuscript writing and graphical work. The manuscript was published in peer-review *Journal of Marine System*: Núñez-Riboni, I. and A. Akimova (2015). "Monthly maps of optimally interpolated *in situ* hydrography in the North Sea from 1948 to 2013", *Journal of Marine Systems* **151**: 15-34.

## Chapter 5

### Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea

AA performed the analyses and text writing. INR was involved in the methods’ development. Marc H. Taylor (MHT) conducted the analyses and writing of the Chapter “Management application”. INR, MHT and Alexander Kempf contributed to the discussion of the main results and writing. The manuscript was published in peer-review journal *PLOS ONE:* Akimova, A., I. Núñez-Riboni, A. Kempf and M. H. Taylor (2016). "Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea", *PLoS ONE* 11(9): e0161917.

# Chapter 6

### Modeling the effects of temperature on the survival and growth of North Sea cod (*Gadus morhua*) through the first year of life

All analyses, text writing and graphical presentation were conducted by AA under supervision of Myron Peck (MP) and Marc Hufnagl (MH). Markus Kreus developed the dispersal module of the biophysical model and supported AA with programming issues. The manuscript was published in a peer-review journal *Fisheries Oceanography:* Akimova, A., M. Hufnagl, M. Kreus and M. A. Peck (2016). "Modeling the effects of temperature on the survival and growth of North Sea cod (*Gadus morhua*) through the first year of life", *Fisheries Oceanography* **25**(3): 193-209.

# Chapter 7

### Hot spots and refuges: The importance of adding spatiotemporal dynamics of predators within biophysical models of marine fish early life stages

AA conducted modelling design and experiments, did all graphical presentation and text writing under close cooperation with MP and MH. The co-authors MP and MH critically reviewed the manuscript. This manuscript is going to be submitted to a peer-review journal *Oecologia*: Akimova, A., M. A. Peck and M. Hufnagl “Hot spots and refuges: The importance of adding spatiotemporal dynamics of predators within biophysical models of marine fish early life stages”

# 3 General introduction

## 3.1 Exploited marine fish stocks and recruitment

Marine fishes are an important food source for humans worldwide and fishing represent one of the oldest recorded activities. Although living aquatic resources are renewable, they are not infinite. Each decade, the demand for fish increases as does our skill at catching fish. Prior to precautionary management, the level of exploitation was too high and many stocks were overfished (i.e., fish populations could not sustain themselves), threatening marine ecosystems (*Jennings and Kaiser, 1998*; *Jackson et al., 2001*). The problem of overfishing became global by the end of the 20th century. Nowadays, the majority of fish stocks is overfished, depleted or is recovering after over-exploitation (*Pauly et al., 2002*; *FAO, 2016*). Therefore, a better understanding of the population dynamics of exploited fish stocks and development of sustainable management strategies based on it are high priority issues for politicians and scientists. One of the most challenging facets of managing fish stocks is understanding the drivers of stock recruitment, i.e. the number of fish offspring surviving to enter the fishery or other reference time in their life cycle (settlement, maturation etc.). Next to reductions caused via fishing, recruitment is the main source of changes in the abundance of fish within a population and is often highly variable from year-to-year (*Fogarty et al., 1991*; *Caley et al., 1996*; *Minto et al., 2008*). Therefore, understanding the processes that control recruitment and gaining the ability to predict year-class success are prerequisite for optimizing sustainable harvesting.

Determining the primary causes of variability in fish recruitment has been a subject of considerable debate in fisheries science since at least the beginning of the 20th century (*Cushing, 1982*; *Blaxter, 1974*; *Chambers and Trippel, 1997*; *Llopiz et al., 2014*). Two major factors have been considered to cause the variability of recruitment: i) the size and condition of the parental stock, and ii) the survival of offspring during early life, which normally refers to a time span between eggs fertilization and the age at which individuals are catchable by corresponding fishery (*Chambers and Trippel, 1997*; *Fuiman and Werner, 2002*; *Jakobsen et al., 2009*). The dynamics of survival and growth of fish early-life stages (ELSs) is believed by many to regulate the year class strength and determine the surplus production of exploited population in many fish stocks. Nonetheless, the processes potentially impacting growth and survival are rarely included in tactical fishery management (*Skern-Mauritzen et al., 2016*). Traditional models developed for resource management during the 1950s are "stock-recruitment" models, i.e. they account mainly for the size of the parental stock as a proxy for the reproductive potential and amount of eggs produced (*Ricker, 1954*; *Beverton and Holt, 1957*;

*Subbey et al., 2014*). In this classical consideration the survival of fish progeny is assumed to be density-dependent and fixed in time. However, long-term observations on exploited stocks demonstrated that, in many cases, stock-recruitment models are unable to explain a significant portions of the observed recruitment variability (*Cushing, 1982*; *Subbey et al., 2014*). Therefore, understanding of the processes affecting survival of early-life stages, the principal regulator of fish recruitment, is critical for the prediction of the future dynamics of exploited fish stocks needed for robust fishery management.

## 3.2 Fish early-life stage mortality

Johan Hjort (1869-1948) was the father of the “early-life history” concept in fisheries science, and was the first to suggest that the observed variations in catches was due to the variable abundance of fish populations and that annual changes in abundance were generated by different rates of mortality mainly experienced during the first year of life (*Hjort, 1914*). Nowadays, it is widely acknowledged that fish early life (egg, larval to age-0 juvenile stages) is a critical period during which natural mortality rates are extremely high (*Chambers and Trippel, 1997*; *Fuiman and Werner, 2002*). It has been estimated that more than 99.9 % of the progeny of a female fish do not survive their first year of life (*Houde, 2002*; *Houde, 2008*). However, the exact mechanisms influencing mortality rates of fish ELSs and their variability at different temporal and special scales still remain opaque for many populations, despite more than a century of extensive research (*Houde, 2008*; *Llopiz et al., 2014*; *Rice and Browman, 2014*).

Numerous processes have been suggested to affect mortality of fish ELSs and thereby recruitment of marine fishes: starvation, dispersal, predation, developmental failure as a result of unsuitable environmental conditions, density-dependent processes at settlement, egg malformation, diseases, parasites, as well as environmental contaminations (e.g. *Sissenwine, 1984*; *Anderson, 1988*; *Bailey and Houde, 1989*; *Cameron et al., 1992*; *Leggett and Deblois, 1994*; *Folkvord, 1997*; *Houde, 2002*; *Krkošek et al., 2013*). Three of these mortality sources – starvation, dispersal/retention and predation – are now widely acknowledged as the main sources of the fish ELS mortality (*Houde, 2008*; *Peck and Hufnagl, 2012*; *Llopiz et al., 2014*). The first two mortality sources have been put forth already in the pioneer study of *Hjort, 1914*. Many decades later, predation mortality was recognized as one of the important or, according to some authors, ultimate source of fish ELS mortality (*Bailey and Houde, 1989*; *Pepin and Shears, 1995*; *Houde, 2002*; *Houde, 2008*).

Starvation mortality have been considered particularly critical for the first-feeding larvae due to their low ability to find and capture their prey, narrow size-spectrum of suitable prey items and the relative short time for unfed larvae to reach the “point-of-no-return”, i.e. the stage of physical deterioration when larvae are still alive but too weak to feed and recover (*Blaxter and Hempel, 1963*; *Blaxter, 1974*). This period of larval first-feeding was called “critical period” by Johan Hjort, who believed that the recruitment success was determined to a large extent by larval survival through their fist-feeding period (*Hjort, 1914*). David Cushing (1920-2008) coupled the concept of “critical period” to the seasonal availability of zooplankton and developed his well-known “match-mismatch” hypothesis. He suggested the temporal overlap between first-feeding larvae and their planktonic food to determine recruitment success in several fish stocks (*Cushing, 1969*; *Cushing, 1990*). The “critical period” and the “match-mismatch” hypotheses have received a considerable support from laboratory and model studies. They are often assumed to underlie observed negative correlations between recruitment and ambient temperature (e.g. *Leggett and Deblois, 1994*; *Beaugrand et al., 2003*; *Platt et al., 2003*; *Kristiansen et al., 2011*; *Huwer et al., 2011*; *Peck and Hufnagl, 2012*; *Daewel et al., 2015*). The “mismatch-match” dynamics and larval survival are driven by an amalgam of intrinsic (spawning strategy of adults, larval foraging behavior and diets, larval physiology) and extrinsic (temperature, ocean currents, turbulence, prey abundance, size-spectrum and patchiness) factors (*Peck et al., 2012* and references there). The interplay between those factors in natural ecosystems are seldom fully understood.

Although starvation is often considered to be an important mechanism determining recruitment success, some studies suggested that direct mortality due to inadequate or suboptimal feeding has been overestimated (e.g. *Houde, 2008*). Fish larvae have been shown to forage more effectively than initially thought and there are several processes (e.g. prey patchiness, micro-turbulence) that support larval feeding even at low, mean prey concentrations (*Kiørboe et al., 1985; Rothschild and Osborn, 1988; MacKenzie et al., 1994*). Furthermore, little is known about suboptimal foraging of fish larvae (Peck et al., 2012; M. Moyano, pers. comm.) and its role for larval survival. It has been hypothesized that poor nutritional condition and increased susceptibility to potential predators might be more important for fish ELS survival than mortality via starvation (*Bailey and Houde, 1989; Houde, 2008; Fiksen and Jorgensen, 2011; Petrik et al., 2014*).

The second source of mortality suggested by Johan Hjort, “aberrant drift”, highlighted the importance of the transport (dispersal) of planktonic fish eggs and/or larvae with oceanic currents toward their suitable nursery areas (*Hjort, 1926*). Later, *Iles and Sinclair (1982)* and *Sinclair (1987)* developed their “member-vagrant” hypothesis based on Hjort’s idea. In general, two mechanisms can be discerned: dispersal, i.e. larval transport away from their spawning sites to nursery areas, and retention, which leads to self-recruitment within a geographically constrained population (*Swearer et al., 1999; Cowen et al., 2000; Paris and Cowen, 2004*). Larval dispersal and retention have been extensively studied for a wide variety of marine organisms and were suggested to be critical mechanisms influencing the recruitment success in many fish populations (*Gaines and Bertness, 1992; Levin, 2006; Gaines et al., 2007; Peck and Hufnagl, 2012*). Dispersal/retention mechanisms are highly complex and depend not only on the variability of the physical processes (advection and diffusion), but also on biological traits of adults (choosing suitable spawning sites) and fish ELSs (e.g. larval size and ability to swim, larval behavior; *Leis, 2006; Levin, 2006; Cowen and Sponaugle, 2009*). Larval dispersal and retention are essential mechanisms influencing the connectivity of marine populations and substantially affect the structure and dynamics of fish stocks (*Eckert, 2003; Pineda et al., 2007; Cowen and Sponaugle, 2009*). Marine connectivity, including processes acting on fish ELSs, has recently received growing attention due to its importance for marine spatial management, e.g., design of marine protected areas or systematic management of fish metapopulations (*Roberts, 1997; Botsford et al., 2001; Palumbi, 2003*).

Predation was intuitively a clear potential source of mortality of fish ELSs due to vulnerability of eggs and small larvae, but its role as a factor regulating the level of recruitment was underappreciated until the 1970-80s. *Cushing (1974)*, followed by *Hunter (1981)* suggested that predation and starvation are the main sources of mortality of fish ELSs, whereas *Bailey and Houde (1989)* were convinced that predation is the single most important process. Marine fish ELSs are consumed by a wide diversity of predators including juvenile and adult fishes, jellyfishes, euphasiids, copepods, and birds (*Möller, 1984*; *Brewer et al., 1984*; *Daan et al., 1985*; *Monaghan, 1992*; *Bailey and Houde, 1989*; *Houde, 2002*). Laboratory experiments and field investigations have suggested that predation is a selective process and depends on the size of predator and prey (*Miller et al., 1988*; *Pepin, 1991*; *Pepin and Shears, 1995*). This implies the decline of overall predation mortality with increased size of fish ELSs in order to be consistent with the observed size-spectrum of marine organisms (*Platt and Denman, 1978*; *Peterson and Wroblewski, 1984*; *Houde, 1997*). However, this decline is not necessarily valid for each individual predator (*Bailey and Houde, 1989*; *Cowan and Houde, 1992*; *Pepin et al., 1992*).

Although predation is acknowledged to be an important regulator of fish ELS survival, many aspects of “predator-prey” interactions are still poorly understood. In many ecosystems, there is still a lack of information about communities of predators consuming fish early-life stages, their diet preference, abundance and spatial distribution (*Houde, 2002*; *Houde, 2008*). The spatial distribution of predators, their movements and spatiotemporal overlap with their prey are recently gaining attention as an important factor controlling the strength of trophic interactions in marine ecosystems, including predation on fish ELSs (*Huse et al., 2004*; *Ciannelli et al., 2007*; *Peck and Hufnagl, 2012*; *Utne and Huse, 2012*; *Greer and Woodson, 2016*). Advancing our knowledge about the variability of the spatiotemporal "predator-prey" overlap and biotic and abiotic factors driving this variability might substantially contribute to our understanding of fish ELS survival and recruitment (*Huse et al., 2004*; *Peck and Hufnagl, 2012*).

Consideration of a single process or mortality source as a determinant of fish ELS survival resulted in a variety of single-factor hypotheses, such as the "critical period" and the "aberrant drift" hypotheses of *Hjort (1914*) and *Hjort (1926)*. Since then, numerous studies demonstrated that what determines the survival of fish early-life stages is probably far more complex and results from an interplay of multiple processes acting over one or several early-life stages (*Anderson, 1988*; *Bakun, 1998*; *Houde, 2008*; *Fiksen and Jorgensen, 2011*; *Peck and Hufnagl, 2012*; *Hare, 2014*). *Peck and Hufnagl (2012)* illustrated some hypothetical scenarios of the interplay between bottom-up, top-down and dispersal processes affecting the abundance, concentration, and growth of a larval fish cohort (Figure 3.1). Scenario S1 depicts the case, when individuals grow fast due to favorable feeding conditions, experience low predation and are transported to their suitable nurseries. This scenario obviously results in the strongest year class (Figure 3.1, panel D). Scenario S2 illustrates the "critical-period" hypothesis, when spatial or temporal mismatch between first-feeding larvae and their prey causes high starvation mortality and the loss of the entire cohort (Figure 3.1, panel D). The "aberrant drift" hypothesis is shown in scenario S3, in which advective processes transport well-growing fish larvae away from their suitable nursery areas causing substantial loss of individuals (Figure 3.1, panel D). Scenario S4 of *Peck and Hufnagl (2012)* represents a case when the cohort experiences favorable feeding conditions as well as high predation resulting in rapid growth but poor recruitment. This situation was suggested to occur in highly productive frontal zones of the world ocean which concentrate prey but also attract predators. The last scenario S5 depicts the situation, when relative poor prey fields result in a slower larval growth and increased vulnerability to predation.

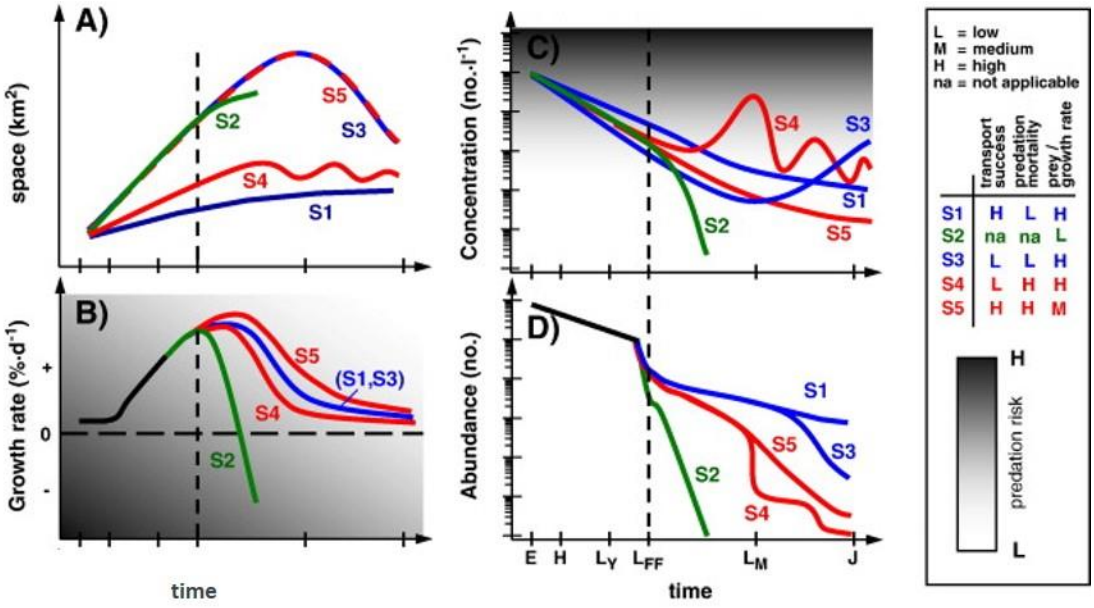

**Figure 3.1. Five hypothetical scenarios of the interplay between bottom-up, top-down and dispersal processes during fish early-life stages, taken from *Peck and Hufnagl, 2012*. Spatial distribution (panel A), growth rate (panel B), concentration (panel C) and abundance (panel D) of a larval fish cohort are shown. Early-life stages are marked on the time axes (E - eggs, H - hatch, $L_y$ - yolk sac larvae, $L_{ff}$ - first-feeding larvae, $L_m$ - metamorphosing larvae, J - juvenile). The magnitude of each interacting process is provided in the legend. Predation mortality is assumed to increase with increasing concentration of individuals within the cohort (panel C) and decrease with individual growth rate and size (panel B).**

## 3.3 Methods of studying recruitment relevant processes

Methods employed to study fish ELSs and recruitment-relevant processes are diverse: from field observations and laboratory experiments, through time series analyses to integrated modeling. Field observations include investigations of the abundance of mature adults and fish pre-recruitment life stages and its spatial and temporal variability (*Heath, 1992*). Long-term monitoring programs on pre-recruitment abundances together with catch data are used in the routine stock assessment (*Hilborn and Walters, 1992*; *Malcolm, 2011*). Time series of assessed stock parameters have been widely used to investigate biotic and abiotic drivers of fish recruitment once fishery and oceanographic data-sets became long enough to perform robust statistical analyses (e.g. *Myers, 1998*; *Planque and Frédou, 1999*; *Gröger et al., 2010*). Time series analyses is a helpful tool to identify responses of a fish population to a set of factors including climate variability, interactions with other species, fisheries or other anthropogenic factors (*Cushing, 1982*; *Stenseth et al., 2004*; *Malcolm, 2011*). Improved data availability has gradually allowed for more complex statistical analyses (e.g. multivariate statistics, spatially-explicit analyses etc.). However, in many cases exact processes behind the observed statistical dependences still remain elusive and demand further exploration. This is particularly the case, when complex (threshold) responses to multiple drivers are observed.

Another fruitful method of studying fish early-life period is investigating fish larvae and juveniles collected in the field, their diets, vertical distribution and condition (e.g. *Buckley, 1984*; *Peterson and Ausubel, 1984*; *Economou, 1991*; *Heath, 1992*; *Munk, 1993*). Field data have often been used to assess predation mortality of fish ELSs in various regions of the world ocean (*Emslie and Jones, 2001*; *Nilsson, 2006*; *Hallfredsson and Pedersen, 2009*; *Kotterba et al., 2014*). Identifying fish ELSs in the gut content of predators is one of the most important sources of quantitative information, despite being criticized as inaccurate due to the rapid digestion of fish larvae and eggs in predator stomach (*Houde, 2002*; *Kotterba et al., 2014*).

Laboratory experiments are mainly used to gain insight into the physiology of fish eggs, larvae and juveniles (e.g. *Giguere et al., 1988*; *Parra and Yúfera, 2000*; *Peck and Buckley, 2008*), including foraging in exogenously feeding life stages (e.g., *Munk, 1995*), swimming activities (e.g. *Coughlin et al., 1992*; *Clark et al., 2005*; *Faria et al., 2009*), responses to changing environment and tolerance limits (e.g. *de Silva and Tytler, 1973*; *Blaxter, 1991*; *Nissling, 2004*; *Peck et al., 2012*), etc. Several papers have performed literature review and interspecific comparison of the major findings of previous laboratory studies (*Pedersen, 1997*; *Peck et al., 2012*; *Llopiz, 2013*). Predation on fish ELSs, however, remains challenging to examine within laboratory experiments and such studies are rare (*Bailey, 1984*; *Pepin et al., 1987*; *Paradis et al., 1996*). Mesocosm experiments or *in situ* experiments under controlled conditions such as predator exclusion cages, are an alternative and promising method of studying predation on fish ELSs (*Bailey and Houde, 1989*; *Fuiman and Gamble, 1988*; *Kotterba et al., 2017*).

Accumulating evidences from field investigations and laboratory experiments have built a solid basis for mathematical modelling of the recruitment processes. Mathematical models aim at a better mechanistic understanding of recruitment with an ultimate goal to predict future recruitment dynamics under natural (climate change) and anthropogenic (fishing, eutrophication, etc.) stressors. A wide array of modeling techniques has been applied: from 0-D single species models to spatially-explicit ecosystem models, and from fully-deterministic to stochastic models (*Plagányi, 2007*; *Pauly and Christensen, 2008*; *Malcolm, 2011*; *Collie et al., 2016*). Individual-based approach, which allowed for modeling of a fish population on an individual-by-individual basis, have gained particular popularity as a tool to study fish early-life history (*DeAngelis and Gross, 1992*; *Van Winkle et al., 1993*; *Grimm and Railsback, 2005*; *Huse et al., 2008*). The reason was the acknowledgement that the survival of fish ELSs varies strongly among fish individuals and this variability probably forms the observed recruitment fluctuations at the population level (*Huse et al., 2008*; *DeAngelis and Grimm, 2014*).

Individual-based (or agent-based) models (IBMs) simulate individuals with a high degree of complexity and biological “realism” to understand how the set of traits (attributes) and behavior of the individuals affect the community as a whole. In fishery science, classical 0D-IBMs have evolved in 3D biophysical models, in which biological life-history IBMs are coupled to hydrodynamic, biogeochemical and particle tracking models (*Werner et al., 2001*; *Miller, 2007*; *ICES, 2009*). Biophysical models have been extensively used to study bottom-up drivers of fish ELS mortality, i.e. starvation and dispersal, and their environmental triggers (*ICES, 2009*; *DeAngelis and Grimm, 2014*; *Peck and Hufnagl, 2012*). As for predation, the majority of previous studies have exploited 0D-IBMs to explore various aspects of predation mortality (e.g. *Pepin, 1989*; *Rice et al., 1993*; *Cowan et al., 1996*; *Letcher et al., 1996*), whereas spatially-explicit simulations have been rarely performed (*Huse et al., 2004*; *Fiksen and Jorgensen, 2011*; *Peck and Hufnagl, 2012*; *Petrik et al., 2014*; *Rose et al., 2015*). As it was mentioned above, the spatial aspects of “predator-prey” interactions are increasingly seen as an important regulator of predation mortality of young fishes. Using biophysical models to study these interactions and their variability at various spatial and temporal scales seems to be a promising approach to gain new insight into predation mortality of fish ELSs (*ICES, 2009*; *Peck and Hufnagl, 2012*).

## 3.4 The North Sea as a case study

The North Sea is a shelf sea surrounded by highly-industrialized European countries who extensively use its waters for shipping, fisheries, wind energy sites, recreation and other commercial activities. It is one of the biologically richest and most productive seas and represents an important fishing ground. It supplies approximately 55% of the total European fishery and the catches were assessed to 3.5 million tons of fish and shellfish in 2013 (*Pinnegar et al., 2016*). Currently about 20 of over 200 fish species inhabiting the North Sea are targeted by commercial fisheries. The targeted species are mostly pelagic fishes such as herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and mackerel (*Scomber scombrus*). The most commercially important demersal species are Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), whiting (*Merlangius merlangus*) and two flatfishes, sole (*Solea solea)* and plaice (*Pleuronectes platessa*). Industrial fisheries (fisheries for non-food purposes) target sandeel (*Ammodytes marinus)*, Norway pout (*Trisopterus esmarkii)*, juvenile herring and sprat.

The intense use of the North Sea has greatly impacted this ecosystem and has catalyzed initiatives to reduce impacts and increase the sustainability of its resources (*OSPAR, 2009; Emeis et al., 2015; Tölle and Colijn, 2016*). The paradigm of sustainable exploitation, including sustainable fisheries, is a highly topical issue. Various management strategies have been applied since 1960 to regulate North Sea fisheries and protect fish stocks from overfishing. Although some of the stocks have recently improved due to the major reduction in the regional fishing mortality, continued effective management remains crucial for this region (*Kelly and Codling, 2006; Cardinale and Svedäng, 2008; O'Leary et al., 2011; Marchal et al., 2016*). Independently of the preferred management paradigm (single-species maximum sustainable yield or ecosystem-based fisheries management), a successful strategy depends on the level of our understanding of the factors and mechanisms driving the recruitment dynamics of exploited fish stocks. Previous studies have shown that recruitment is often correlated to environmental conditions in the North Sea (e.g. *Planque and Frédou, 1999; Fox et al., 2000; Arnott and Ruxton, 2002; Nash and Dickey-Collas, 2005; Ottersen et al., 2013*). Various sources of fish ELS mortality have been hypothesized to underlie these correlations: starvation mortality for cod (*Beaugrand et al., 2003; Nicolas et al., 2014; Daewel et al., 2015*), herring (*Payne et al., 2009; Hufnagl et al., 2015*), sandeel (*Arnott and Ruxton, 2002*), dispersal mortality for plaice (*Rijnsdorp et al., 1995; Hufnagl et al., 2013*) and sole (*Lacroix et al., 2013*), predation mortality for cod (*Kempf et al., 2009; Kempf et al., 2013; Hjermann et al., 2013*), herring (*Lynam et al., 2005*), and plaice (*Fox et al., 2000; Nash and Geffen, 2012*). However, many of these hypotheses remain to be rigorously tested. Moreover, some correlations are rather weak and/or unstable in time, suggesting that we lack a full understanding of the driving mechanisms and/or their interplay.

This thesis aimed to address two gaps in our understanding of the recruitment dynamics of commercially important fish species in the North Sea. One of the gaps concerns the direct and indirect influence of physical processes on recruitment and changes in stock abundance. The majority of previous ecosystem and fishery studies have used observations of environmental parameters either at a certain measurement point or averaged over the whole basin (e.g. *Fox et al., 2000*; *Planque and Frédou, 1999*; *Gröger et al., 2010*; *Pécuchet et al., 2014*). Thereby, they implicitly assumed the North Sea hydrography to be homogeneous and to vary in time as a single body. However, oceanographic studies based on *in situ* observations and hydrodynamic models have demonstrated that the hydrography of the North Sea is heterogeneous and different processes drive the variability of temperature and salinity in different parts of this shelf sea (e.g. *Lee, 1980*; *Becker and Pauly, 1996*; *Becker et al., 1997*; *Dippner, 1997*; *Heyen and Dippner, 1998*; *Hjøllo et al., 2009*). Recently, two papers have synthesized previous and new findings about low-frequency (inter-annual to inter-decadal) variability of temperature (*Mathis et al., 2015*) and salinity (*Núñez-Riboni and Akimova, 2017*) in the North Sea. Temperature spatiotemporal variability has been shown to be driven by: i) surface heat fluxes from the atmosphere in the southern North Sea, ii) vertical mixing in the central and northern North Sea, iii) advective heat fluxes in the northern North Sea, English Channel, and along the Norwegian Trench (*Mathis et al., 2015*). As for salinity, following mechanisms were found to regulate its low-frequency variability: i) the river run-off from continental Europe in the southern and eastern North Sea, ii) advection of remote variations of salinity in the eastern North Atlantic in the north-western North Sea, iii) the Neva discharge in Skagerrak, iv) the wind-induced advection of the Atlantic waters off the Norwegian coast (*Núñez-Riboni and Akimova, 2017*). In my opinion, addressing the observed heterogeneity of the North Sea hydrography in the analyses of the environmental influence on fish stocks may help to more accurately identify physical processes driving the variability of the fish stocks and their productivity and possibly improve our ability to predict them. Better understanding of the environmentally-driven changes in stocks productivity is particularly important given the observed and expected effects of climate change in the North Sea region (*Quante and Colijn, 2016*).

A better understanding of the role of predation mortality of fish ELSs as a driver of recruitment variability was the second aim of this thesis. The North Sea ecosystem, similar to the majority of marine ecosystems, is highly complex and fish species interact at various trophic levels (as predators and/or prey) depending on their life stage (*Daan et al., 1990; Frederiksen et al., 2006; Quante and Colijn, 2016*). Planktivorous fishes, such as herring, sprat, and mackerel can consume a substantial amount of fish eggs and larvae (*Daan et al., 1985; Dahl and Kirkegaard, 1986; Segers et al., 2007; Van Ginderdeuren et al., 2013*). Demersal species, such as cod, whiting, grey gurnard (Eutrigla gurnardus) and saithe, prey actively on demersal young-of-the-year fishes including cannibalism (*Daan, 1989; Hislop et al., 1997; Greenstreet, 1996; Floeter and Temming, 2005; Temming et al., 2007*). The role of predation mortality in recruitment variability has been rarely assessed. This is partially related to notorious difficulties to observe fish ELSs in the field and to assess predation on fish eggs and larvae. Even in the North Sea, one the most thoroughly- studied regions, such observations and estimates are very scarce. Mathematical models seem to be a promising tool to help guide the generation of hypotheses and reveal the most urgent data gaps. However, only few modelling studies have dealt with predation mortality on fish ELSs in the North Sea so far (e.g. *Floeter et al., 2005; Kempf et al., 2010; Speirs et al., 2010*).

## 3.5 The Atlantic cod as a model species

Cod is the common name for the genus *Gadus* of demersal fishes that belongs to the family Gadidae (gadoids). Atlantic cod (*Gadus morhua*) and Pacific cod (*Gadus macrocephalus*) are the most widespread species within this genus. Atlantic cod represents one of the most valuable commercial fishes and its stocks are spread all over the North Atlantic: Georges Bank, Newfoundland, West Greenland in the West Atlantic; Celtic Sea, North Sea, Iceland, Faroes, Baltic Sea stocks in the east Atlantic; Norwegian coastal stock in the Atlantic sector of the Arctic Ocean (*ICES, 2005*). Fisheries on cod can be tracked back to the Viking period (around AD 800) and has a curious history, including so called "cod wars", confrontations between Britain and Iceland regarding the control over fishing areas in the North Atlantic (*Ingimundarson, 2003*; *Jóhannesson, 2004*; *Wikipedia, 2017*). By the middle of the 20th century, most of the coastal cod stocks were heavily exploited and strict management strategies were suggested to prevent stock collapses. Despite this management effort, several cod stocks collapsed (e.g. dropped below 5% of their maximum historical biomass) between 1990s and early 2000s and some of them have not fully recovered (*ICES, 2005*; *Olsen et al., 2011*). The "Guardian" described the collapses of cod stocks as "one of the most disastrous examples of overfishing" (*Smith, 2015*). The historic importance of cod and the severe collapses of its stocks pushed forward an intensive research. Nowadays, Atlantic cod can be referred as one of the most studied marine fish species (*ICES, 1994*; *Planque and Frédou, 1999*). For example, a Corporative Research Report (CRR) on Atlantic cod published in 2005 by experts of the International Council for the Exploration of the Sea (ICES) contains almost 2000 references, including peer-reviewed papers, reports and book chapters (*ICES, 2005*). A substantial part of this enormous body of literature deals with diverse aspects of the reproductive biology of cod. It has been shown that recruitment is weakly coupled to the size of the reproductive stock in the majority of cod stocks. Therefore, processes taking place during the early-life period have been suggested to drive the recruitment variability of cod (e.g. *Buckley and Lough, 1987*; *ICES, 1994*; *Köster and Möllmann, 2000*; *Garrison et al., 2000*; *Beaugrand et al., 2003*).

The North Sea stock of Atlantic cod (further on North Sea cod) used to be one of the largest cod stocks, together with the Norwegian and Georges Bank stocks (*ICES, 1994*). In the begging of 1960s an upsurge of cod recruitment and stock biomass in the North Sea was observed (*Cushing, 1984*). This upsurge was accompanied by an increase in the biomass of other gadoid species (haddock, whiting, saithe and Norway pout) and it is now referred as the "gadoid outburst". In the 1980s, the North Sea cod stock started to rapidly decline and dropped below its safe biological limit by the early 2000s (*Horwood et al., 2006*). This stock depletion is believed to be caused by two major factors: heavy exploitation and a prolonged recruitment failure (*Hislop, 1996*; *Cook et al., 1997*).

According to long-term observations, recruitment of North Sea cod is only weakly correlated to the size of its spawning stock (*Olsen et al., 2011*). The variability of other aspects of the parental stock (e.g., spatial distribution, age structure or spawning time) has been considered to be a factor potentially influencing cod recruitment in the North Sea (*Rochet, 2000*; *Morgan et al., 2013*; *Nicolas et* *al., 2014*). Moreover, starvation (*Cushing, 1984*; *Beaugrand et al., 2003*; *Daewel et al., 2015*) and predation (*Floeter et al., 2005*; *Kempf et al., 2010*; *Hjermann et al., 2013*; *Minto and Worm, 2012*) mortalities of cod ELSs have been hypothesized to affect recruitment. To my knowledge, dispersal or retention have never been considered to be important, because North Sea cod does not appear tightly constrained to fixed nursery grounds.

The importance of starvation and the "match-mismatch" dynamics for recruitment of North Sea cod has been suggested for the first time by *Cushing (1984)* and later confirmed by *Rothschild (1998)*. A year later, *Planque and Frédou (1999)* reported significant correlations between water temperature at the time of spawning and the strength of cod recruitment in each of nine cod stocks in the North Atlantic, including the North Sea. *Beaugrand et al. (2003)* brought the findings of *Cushing (1984)* and *Planque and Frédou (1999)* together by suggesting two mechanisms causing bottom-up control of cod recruitment. They postulated that the observed changes in temperature affected zooplankton community in the North Sea and thereby the survival of larval/juvenile cod which depend on specific components of the zooplankton community. The importance of the "match-mismatch" dynamics for cod recruitment was also suggested from the results of biophysical model simulations conducted by *Daewel et al. (2011), Kristiansen et al. (2011), Kristiansen et al. (2014), Daewel et al. (2015)*.

As for predation, numerous field studies have demonstrated that substantial amount of cod eggs, larvae and juveniles are consumed by planktivorous and piscivorous predators in the North Sea (e.g. *Daan et al., 1985*; *de Gee and Kikkert, 1993*; *Greenstreet et al., 1997*; *Floeter and Temming, 2005*; *Temming et al., 2007*). Several studies have attempted to quantify predation mortality and estimate its consequences for cod recruitment in the North Sea. *Floeter et al. (2005)*, *Kempf et al. (2009)* and *Kempf et al. (2013)* showed a significant effect of predation of adult cod, grey gurnard and whiting on cod recruitment. *Speirs et al. (2010)* demonstrated the importance of herring predation on cod eggs and larvae using a 0-D size-structured trophic model. Their findings were confirmed by *Hjermann et al. (2013)*, who used field observations and spatially-explicit time-series analyses. Previous empirical studies suggested that the spatial overlap between juvenile cod and its predators can be an important regulator of the magnitude of mortality of cod pre-recruits (*Kempf et al., 2009*; *Kempf et al., 2013*). To my knowledge, there is no observations that would enable analyses of the spatial co-variability of cod eggs and larvae and their predators. Previous biophysical models of ELS mortality of cod utilized spatially invariant predation and ignoring spatial aspects of predator-prey interactions (*Kristiansen et al., 2011*; *Gallego, 2011*). Therefore, the spatial dynamics of cod predators and predation mortality of cod ELSs in the North Sea are poorly known.

## 3.6 Thesis objectives

This thesis aimed at gaining a better understanding of the recruitment dynamics of marine fishes. Both biotic and abiotic processes affecting survival of fish ELSs were addressed with a focus on commercially-important fishes in the North Sea, particularly North Sea cod. The main objective was to investigate how the factors and mechanisms potentially regulating survival of fish pre-recruits may vary in space and whether this spatial variability affects year-to-year changes in the year class success (recruitment) of commercially exploited marine fishes.

The first objective of the thesis was to study the spatially-explicit influence of the environmental conditions on the abundance and recruitment of nine fish stocks in the North Sea, i.e. Atlantic cod, Atlantic herring, European sprat, European plaice, common sole, haddock, Norway pout, whiting and saithe. For this purpose monthly maps of the North Sea hydrography over the period of several decades were reconstructed based on the available observations (Chapter 4). Based on this hydrography, the environmental influence on fish stocks was explored by means of the spatially-resolved cross-correlation analysis (Chapter 5). Chapters 6 and 7 aimed at studying spatiotemporal variability of predation mortality of cod ELSs in the North Sea. A spatially-explicit IBM of cod eggs, larvae and juveniles was developed. The goal of Chapter 6 was to explore how temperature influences the survival of cod if temperature effects on the growth rate of cod ELSs and on the consumption rate of its main predators are taken into account. The model study in Chapter 7 was designed to study how changes in environmental conditions, in the biomass and the spatial distribution of cod predators affects the spatial and inter-annual variability of cod ELS survival in the North Sea.

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# 4 Monthly maps of optimally interpolated in situ hydrography in the North Sea from 1948 to 2013

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## 4.1 Abstract

We used a statistical model mainly based on optimal or Gauss-Markov interpolation (OI) to produce monthly maps of in situ hydrography in the North Sea through 66 years (from 1948 to 2013) with a resolution of 0.2° × 0.2°. The *in situ* hydrography data are approximately 430,000 hydrographic profiles and aggregated thermosalinograph data from various international data bases. Duplicates, outliers and vertical density instabilities were removed. Regions with poor OI estimates were replaced with a harmonic reconstruction arising from the most reliable OI estimates. Adjustments for vertical density stability were based on the standards of the World Ocean Atlas. We mapped at 54 depth levels through the water column, focusing on surface and bottom hydrography because this type of maps is of particular interest for ecosystem and fishery research. Average OI temperature and salinity expected errors at the surface are 0.3°C and 0.1, respectively. OI errors decrease with depth following decrement of signal and noise variances and apparently independent of the data amount (indicating a good data coverage). Alternative error estimates were obtained with the Median Absolute Deviation between our hydrography estimates and time series excluded from the analysis and are on average 0.3°C and 0.1 salinity units. While our product seems limited for analysis of variability on monthly and seasonal time scales, particularly in the regions of large variability, it is suitable for studies of inter-annual and decadal variability. A comparison with two alternative analyses (KLIWAS and SODA) is discussed. As direct application of our results, we present a new hydrographic climatology of the North Sea at various depths with an improved effective resolution.

## 4.2 Introduction

Maps of oceanographic properties have proven to be of great utility as, for example, boundary and initial conditions in numerical circulation models, for verification of ocean numerical simulations and planning of oceanographic expeditions (*Locarnini et al., 2010*). Gridded hydrography is particularly important for climate studies, which make use of large amounts of maps spanning various decades (see for instance *Kaplan et al., 1998*). The North Sea (Figure 4.1), due to its geographical location, is one of the most extensively explored and exploited seas in the world. Previous climatic studies in the North Sea have shown the need of gridded hydrography in this region spanning a long period (*Becker and Pauly, 1996*; *Becker et al., 1997*).

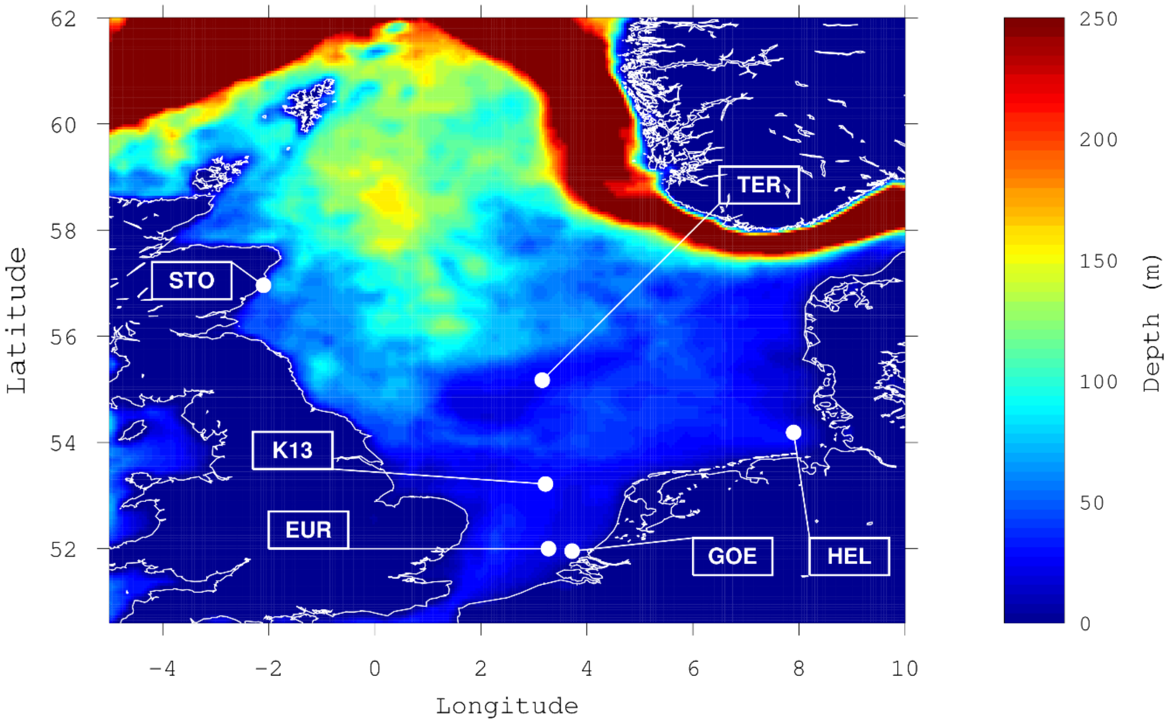

**Figure 4.1: Study area and ETOPO1 bathymetry decimated to our grid resolution. The position of six sampling stations (Table 4.2) are shown, from where independent time series were taken to validate our analysis.**

Spatially resolved maps of surface and bottom hydrography in the North Sea have shown to be also useful for ecosystem and fisheries studies because they describe habitats of pelagic and demersal fishes, respectively (*Ehrich et al., 2009*; *Kempf et al., 2013*). Such maps also indirectly provide information about life conditions of the fish early-life stages and food availability, which were shown to be particular sensitive to water temperature (*Planque and Frédou, 1999*; *Beaugrand et al., 2003*; *Hufnagl and Peck, 2011*). The seasonal spawning and migration, stage-specific development, overwintering and feeding strategies of marine organisms, as well as the specific time-scales of fisheries and ecosystem sampling, demand maps of hydrography at quarterly or monthly resolution (*ICES, 2010*; *ICES, 2015*). On the other hand, unless using a topography-following vertical coordinate, a good resolution for the bottom layer can only be achieved with a relatively high vertical resolution.

Due to climate change, the influence of physical variables on ecosystems at the long time-scales of climate studies is gaining increasing importance for fisheries biology and management (*Daw et al., 2009*). Ecology and fisheries studies related to climate change demand large amounts of gridded hydrography spanning a long period of time, like decades, with a relatively high sampling frequency, like months (*Berx et al., 2011*). Currently there is not a satisfactory product for such studies in the North Sea, at all depths, with high resolution and freely available to the scientific community:

1. Satellites provide maps of sea surface temperature (SST) at weekly or even daily basis for various decades (*Reynolds and Smith, 1994*; *Reynolds et al., 2002*; *Høyer and She, 2007*) but no information about deeper water layers or about salinity (until now). Furthermore, various ecosystem, fisheries and climate studies demand maps of water characteristics from years previous to the satellite era (*Berx et al., 2011*), which started in the 1980s.

2. Direct models are relatively computationally cheap methods yielding long-term hincasts of hydrography (for instance, in the North Sea, the Hamburg Shelf Ocean Model, HAMSOM; *Backhaus, 1985*). Such models are valuable tools for variability and dynamical studies at climatic time-scales but modelled hydrography differs considerably from observed values (*Delhez et al., 2004*). Even though in recent modelling studies (*Hjøllo et al., 2009*; *Meyer et al., 2011*) a fair representation of temperature could be achieved, salinity variations are still poorly represented due to the use of long-term monthly mean river run-off (*Meyer et al., 2011*) or fluxes through open boundaries (*Hjøllo et al., 2009*). Additionally, approaches more directly related to observations are also relevant to validate direct model runs.

3. High-resolution inverse models or assimilation schemes demand large computational resources, allowing analysis of only few years. Therefore, such studies in the North Sea commonly focus on short-term forecasting (*Siddorn et al., 2007*; *Fu et al., 2011*) and not on multi-decade hincasts. Recent ocean reanalyses spanning various decades have as domain the world ocean (for instance the Simple Ocean Data Assimilation, SODA; *Carton and Giese, 2008*), achievable only with a relatively coarse space and vertical resolution (0.5° and 24 levels in the North Sea). Furthermore, such elaborate ocean reanalyses depend on model parameterizations, which simplify complex and only partially understood physical phenomena. This makes, again, more simple methods a valuable first step for comparison of results.

These notions point to the need in the North Sea of a computationally cheap but robust gridding of in situ hydrography. One such method is Optimal Interpolation (OI) or Gauss-Markov estimation (*Gandin and 1963*). OI has been widely used in oceanography to map current velocities, stream function and dynamic height (*Freeland and Gould, 1976*; *Bretherton et al., 1976*; *McWilliams, 1976*; *Hiller and Kaese, 1983*; *Davis, 1985*; *Denman and Freeland, 1985*; *Chereskin and Trunnell, 1996*), in situ hydrography (*Roemmich, 1983*; *Denman and Freeland, 1985*; *Kaplan et al., 1998*; *Meyer et al., 2011*; *Toompuu and Wulff, 1995*; *Hosoda et al., 2009*), tracers (*Sarmiento et al., 1982*), SST in the world ocean (Clancy et al 1990; *Reynolds and Smith, 1994*; *Reynolds et al., 2002*) and, with higher resolution, only in the North and Baltic Seas (*Høyer and She, 2007*).

The goal of this study was to develop a statistical model, mainly based on OI, to estimate monthly maps of in situ temperature and salinity in the North Sea with a horizontal resolution of 0.2°×0.2°, from 1948 to 2013. Looking forward to ecology and fisheries studies, we map at various depth levels with a high vertical resolution to satisfactorily resolve bottom hydrography in the horizontal. Our end product will be available to the scientific community linked in the web portal of the Working Group on Operational Oceanographic Data Products for Fisheries and the Environment (WGOOFE) of the International Council for the Exploration of the Seas (ICES), conforming to the recommendations by *Berx et al. (2011)* relating to data format and meta-data.

## 4.3 Data

We analyze approximately $4.3 \cdot 10^5$ hydrographic stations collected from 1948 to 2013 in the region from 50.6°N to 62°N and from 5°W to 10°E (Table 4.1 and Figure 4.1). These are mostly high resolution Conductivity-Temperature-Depth (CTD) profiles, expendable Bathythermograph (XBTs) profiles, and thermosalinograph and bottle data. We exclude data from the Irish Sea, Danish straits and Kattegat to avoid influence of waters separated by land masses. The data were provided freely by the World Ocean Database 2009 (WOD09; *WOD, 2013*), the Integrated Climate Data Center (ICDC) of the University of Hamburg (*ICDC, 2013*), Coriolis (*Coriolis, 2013*), ICES (*ICES, 2013*) and the German Federal Maritime and Hydrographic Agency (Bundesamt für Seeschifffahrt und Hydrographie; BSH).

**Table 4.1. Number of hydrographic profiles and aggregated thermosalinograph data used in the present study, from 1948 to 2013 in the North Sea (50.6°N to 62°N and 5°W to 10°E). Data sources are shown in the first column. WOD stands for World Ocean Database, ICDC for Integrated Climate Data Center, XBT for expendable Bathythermograph, MBT for mechanical Bathythermograph, ICES for International Council for the Exploration of the Sea and BSH for Bundesamt für Seeschifffahrt und Hydrographie (the German Federal Maritime and Hydrographic Agency). Note many profiles are both temperature and salinity profiles.**

| Data source | Temperature profiles | Salinity profiles | Total profiles |
|---|---|---|---|
| **WOD** | 271490 | 214879 | 275009 |
| **ICDC XBT** | 59 | 0 | 59 |
| **ICDC MBT** | 1058 | 0 | 1058 |
| **Coriolis** | 970 | 967 | 971 |
| **ICES** | 30143 | 30791 | 32065 |
| **BSH** | 103106 | 98789 | 117152 |
| **Total** | 406826 | 345426 | 426314 |

We used the 1 arc-minute global bathymetry ETOPO1 of the National Oceanic and Atmospheric Administration (NOAA) of the USA (*Amante and Eakins, 2009*) as mask for the bottom hydrography maps.

To assess the quality of our results, we compared our maps with the following products: high-frequency time series of temperature and salinity from six sampling stations in the North Sea (Figure 4.1; Table 4.2), the global ocean reanalysis SODA (*Carton and Giese, 2008*; *SODA, 2013*) and version 1.1 of quality-controlled non-gridded observations from KLIWAS (*Bersch et al., 2013*). SODA and KLIWAS use data sets mostly overlapping ours. The time series from the sampling stations were only incorporated in our analysis for a final run after the validation.

**Table 4.2 High-frequency time series of temperature and salinity from six sampling stations in the North Sea used to validate AHOI. The second column shows the abbreviations used in the text. The Stonehaven time series were provided by Marine Scotland Science, the time series from the platforms Terscherlling (235 km offshore), K13a, Euro and Goeree (20 km offshore) were provided by the Netherlands „Ministerie von Verkeer en Vaterstaat" (http://live.waterbase.nl) and the Helgoland time series by the Bundesamt für Seeschifffahrt und Hydrographie, Germany. Positions of the stations are shown in Figure 4.1.**

| Time series | Abbr. | Latitude | Long. | Depth(s) | Initial year | Final year | Reference |
|---|---|---|---|---|---|---|---|
| Stonehaven | STO | 57.0°N | 2.1°W | 1 and 45m | 1997 | 2012 | *Bresnan et al., 2009* |
| Terscherlling | TER | 55.2°N | 3.2°E | "Surface" | 1988 | 2013 | |
| K13a | K13 | 53.2°N | 3.2°E | "Surface" | 1992 | 2013 | |
| Euro | EUR | 52.0°N | 3.3°E | "Surface" | 1989 | 2012 | |
| Goeree | GOE | 52.0°N | 3.7°E | "Surface" | 1975 | 1995 | |
| Helgoland Roads Kabeltonne | HEL | 54.2°N | 7.9°E | 1 m | 1962 | 2010 | *Gerdts et al., 2004* |

Finally, SST data from NOAA (NOAA_OI_SST_V2; *NOAA, 2013*) were used to estimate the integral time scale of the temperature field.

## 4.4 Quality controls and preprocessing

XBT data were corrected from the free fall bias by the data providers following *Gouretski and Reseghetti (2010)*. Profiles from two different data sources with identical geographical position to the first decimal (corresponding to approximately 4 km distance) and times within 6 hours were considered as duplicates (roughly every third profile). Because such duplicates lead to an overestimation of the interpolation accuracy, they were rejected by choosing only one of the data sources.

Data with temperatures beyond -1.2 and 25°C and salinities above 36 were rejected. Vertically unstable profiles due to measurement error (order of 1000 profiles) were rejected following *Locarnini et al. (2010)*. Further elimination of outliers will be described in Chapter 4.5.3 below because it partially depends on other steps of the analysis (vertical interpolation and OI).

Profiles with lowest sampled depths exceeding ETOPO1 by too much were considered as having a wrong position and were rejected. Improving over *Berx and Hughes (2009)* and *Bersch et al. (2013)*, our threshold between ETOPO1 and profile depths was proportional to the magnitude of the ETOPO1 bathymetry gradient $|\nabla B|$. This approach follows the notion that profile positions (i.e., the GPS of the vessel) and ETOPO1 are both inaccurate. Near sharp bathymetry features, like underwater channels, Norwegian fjords and Norwegian trench, the position inaccuracies can be translated as large apparent depth differences between the profile depth and ETOPO1. Our method avoids erroneously rejecting these profiles by taking $|\nabla B|$ into account. Thus, we low passed $|\nabla B|$ with a 20-point Hanning window and eliminated profiles exceeding ETOPO1 by more than $N \cdot |\nabla B|$. We chose N=2° empirically, by plotting the positions of the removed profiles for various values of N until obtaining a relatively homogeneous spatial distribution independent of steep topographic features. Additionally, we demand a minimum depth difference of 25 m (i.e., $N \cdot |\nabla B| \geq 25$ m; based on *Berx and Hughes (2009)*, to avoid eliminating correct profiles in regions with flat bathymetry, where $N \cdot |\nabla B|$ tends to zero. Roughly 1500 profiles were eliminated with these measures.

Data from moored buoys were monthly averaged because observations at the same location contributed little to the interpolation quality but slowed down the computation. Similarly, high-resolution ICES thermosalinograph data were aggregated in 0.25° × 0.25° boxes within the same month.

The vertical distribution of the quality controlled data is shown in Figure 4.2. Roughly only $2.7\times10^5$ temperature and $1.7\times10^5$ salinity profiles passed the quality checks. Because the CTD casts seldom start immediately below the surface and thermosalinograph data are taken deeper than 5 m, the largest data amount down the water column is between 5 and 10 m depth (Figure 4.2, panels a and d). Below 10 m, the data amount decreases with depth (in agreement with reduction of the effective basin area with depth).

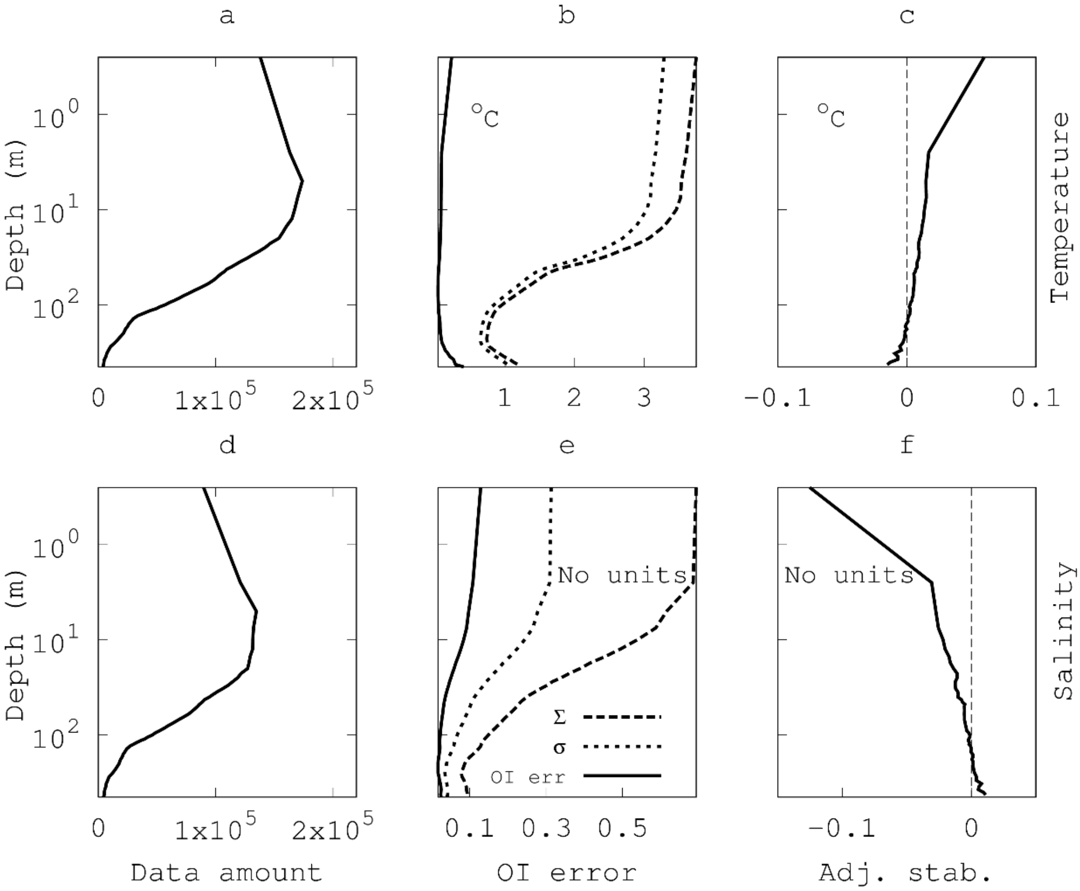

**Figure 4.2. Average values of some key quantities of AHOI as function of depth. Upper panels are related to temperature, lower panels to salinity. First panels from the left (a and d): Amount of quality controlled data. Middle panels (b and e): OI error (continuous curves; Eq. 4.14), square root of signal $\sigma^2$ (dotted curves; Eq. 4.15) and total $\Sigma^2$ (dashed curves) variances. Right panels (c and f): Adjustment for stability (Chapter 4.5.5). Units are shown inside each panel. The depth scale is logarithmic.**

## 4.5 Analysis

To produce monthly maps of *in situ* hydrography in the North Sea, we have developed in this study a statistical model based on these 5 steps:

1. Vertical interpolation of hydrography profiles on our model depth levels;
2. Identification and removal of outliers partially based on optimal interpolation (OI);
3. Mapping of hydrography using OI, independently for each variable (temperature and salinity) and for each depth level;

4. Adjustment of poor OI estimates with an harmonic reconstruction arising from the most reliable OI estimates;
5. Adjustment of the OI estimates for density stability based on the World Ocean Atlas methods;

In the present chapter, we describe these steps and the model validation method, with most details of the OI in an appendix at the end of the article.

### ***4.5.1 Vertical interpolation of data on depth levels***

The vertical correlation of hydrography in the North Sea drops to zero in few meters due to the seasonality of the vertical stratification, making a vertical interpolation difficult. Therefore, analyzing the data at different depth levels independently from each other should preserve stratification better than interpolating between levels (*Janssen et al., 1999*).

We chose 54 depth levels at 2.5 m intervals in the surface 50 m, 5 m intervals between 50 and 130 m, 10 m intervals between 130 and 200 m and 25 m intervals below 200 m. To assign data to these depth levels we followed these steps: we averaged observed values only if they were within 0.5 m above or below a depth level (43% of the cases). Otherwise we interpolated the profiles based on the method of a reference curve to minimize profile overshooting (*Reiniger and Ross, 1968*; *Locarnini et al., 2010*): Lagrangian interpolation (*Emery and Thomson, 2004*) was applied if at least three profile data points were available and homogeneously distributed (34% of the cases). Data points were considered homogeneously distributed when the standard deviation of their depth differences was smaller than their mean depth difference. When this was not the case, linear interpolation was used (23% of the cases).

### ***4.5.2 Optimal estimates***

We obtain an optimally interpolated (OI) hydrography value $\hat{Y}$ (or OI estimate) through the main OI equation (*Gandin, 1963*; *Bretherton et al., 1976*):

$$\hat{Y} = \rho \cdot A^{-1} \cdot y + \bar{Y}, \qquad 4.1$$

where $y$ is a column vector of observation anomalies with respect to the mean field $\bar{Y}$ and $\rho$ is an auto-correlation row vector between observations and estimate point. In our case, the anomalies arise from the data described in Table 1. The matrix $A$ is defined as:

$$A = R + s \cdot I, \qquad 4.2$$

where $R$ is the auto-correlation matrix between anomalies $y$, $s$ is an estimate of the noise-to-signal ratio of the hydrography field and $I$ is the identity matrix. We describe in detail how all these quantities were calculated from the observations in the appendix at the end of the article.

### *4.5.3 Removal of outliers*

Additionally to the profile quality controls (Chapter 4.4), we identified and eliminated outliers in each depth level as follows.

In a first step, we calculated upper and lower bounds for temperature by averaging the largest and smallest 5% quality controlled observations inside overlapping neighborhoods of 1° around the grid points. The upper salinity bound was calculated also with 5% of the data, while for the lower salinity bound we took 10%. We then truncated the dataset by removing observations outside these bounds.

In a second step, we followed a "buddy check" proposed by *Gandin (1963)* (his Section 3.5 in Chapter 5): we compared each observation $Y$ with its OI estimate $\hat{Y}$ (Eq. 4.1) obtained with nearby observations but excluding $Y$ itself. For each $\hat{Y}$, we considered only 20 observations within a space-time ellipsoid centered on the estimate point. The ellipsoid radii were incremented proportional to the e-folding distances and times of first estimates of the covariance functions (Chapters 4.9.2 and 4.9.3) until finding the 20 observations, with at least 15 belonging to the same month as $Y$. This restriction was to avoid including only non-synoptic observations, which leaded often to OI estimates $\hat{Y}$ strongly differing from neighboring estimates even if close in space.

Observations differing from their OI estimate more than a prescribed threshold were removed as outliers. We chose as threshold 1.6° C and 0.8 salinity units based on obtaining well-behaved auto-correlation functions (reasonable noise variances and noise-to-signal ratios) and smooth mean fields from the data without outliers (i.e., repeating steps in Chapters 4.9.1 to 4.9.3). Both methods to eliminate outliers lead to removing roughly 7.3% of temperature and 6.5% of salinity observations. Most outliers were found in regions of high variability, like the German Bight, close to river mouths and the Norwegian trench region. On the vertical, the maximum number of outliers was in the near-surface layers.

After removing outliers from each depth level $d$, the data have been mapped on a regular grid using Eq. 4.1 (details in Chapter 4.9.4).

### 4.5.4 *Harmonic adjustment for regions with scarce data*

In regions with scarce data, our OI estimates $\hat{Y}$ are close to the long-term climatology $Y^d$ (Chapter 4.9.1). To improve these estimates, we first performed a first complete interpolation from 1948 to 2013 to obtain alternative hydrography estimates $\widehat{Y_H}$ from a harmonic analysis of the most reliable OI estimates. Then we replaced poor OI estimates $\hat{Y}$ with $\widehat{Y_H}$ using the following linear relation on the OI errors $\hat{e}$ (Eq. 4.13) for each depth level $d$:

$$\hat{Y}_c(\hat{e}) = \frac{\hat{Y}_H \cdot (\hat{e}^2 - \hat{e}_0^2) + \hat{Y} \cdot (\hat{e}_1^2 - \hat{e}^2)}{\hat{e}_1^2 - \hat{e}_0^2}, \qquad \hat{e}_0 \leq \hat{e} \leq \hat{e}_1 \qquad 4.3$$

where $\hat{e}_0$ and $\hat{e}_1$ are the minimum and maximum OI errors involved in the correction: for OI errors equal to or smaller than $\hat{e}_0$ no correction was performed, i.e. $\hat{Y}_c(\hat{e} \leq \hat{e}_0) = \hat{Y}$ and for OI errors equal to or exceeding $\hat{e}_1$, the OI estimate $\hat{Y}$ was completely replaced by $\widehat{Y_H}$, i.e. $\hat{Y}_c(\hat{e} > \hat{e}_0) = \hat{Y}_H$. We considered OI estimates as poor if the corresponding OI errors were larger than 50% of the signal variance $\sigma^2$ (Denman and Freeland 1985), i.e. $\hat{e}_0^2 = 0.5$. We arbitrarily chose $\hat{e}_1^2 = 0.8$ (corresponding to 80% of the signal variance).

$\hat{Y}_H$ was reconstructed using amplitudes and phases of 5 harmonics with periods of 8, 5, 2.5, 1 and 0.5 years. The amplitudes and phases were obtained by fitting harmonic functions with the fixed periods to at least 15 OI estimates with $\hat{e}^2 < 0.5$ using the downhill simplex method (*Nelder and Mead, 1965*). Amplitudes and phases obtained for the annual harmonics (not shown) were similar to those of *Berx and Hughes (2009)* (their Figures 2 and 3). Approximately 30% of the salinity and only few temperature OI estimates were replaced by the harmonic reconstruction $\hat{Y}_H$.

### 4.5.5 *Adjustment for vertical density stability*

While mapping each depth level independently is a way of preserving stratification, it can also create vertical density instabilities in the gridded maps (*Janssen et al., 1999*; *Berx and Hughes, 2009*). One reason for such instabilities is that there are much more temperature than salinity data (*Locarnini et al., 2010*). A further reason in our particular case is temperature and salinity being interpolated with different auto-correlation functions. Because our time scales are of roughly one month (time enough for the water column to re-stratify), such instabilities represent unphysical conditions which must be corrected. Our correction was based on *Jackett and Mcdougall (1995)* and *Locarnini et al. (2010)*, but we weighted temperature and salinity not depending on their vertical gradients but proportionally to the vertically averaged OI errors. This approach follows the plausible notion that the less accurate variable is more probable to be responsible for the vertical density instabilities and should be more corrected than the more accurate variable.

In the stability adjustment we assumed that all our data have depth as vertical variable. Because most profiles in the North Sea are shallower than 200 m, the few cases where the vertical variable could be pressure should have little impact on our stability correction.

### *4.5.6 Comparison with other products*

To make a clear distinction with the non-adjusted OI estimates (without harmonic correction and stability adjustment), in what follows we call our statistical model and its output Adjusted Hydrography Optimal Interpolation (AHOI). To assess its performance, we compared our results with two other products: KLIWAS (*Bersch et al., 2013*) and SODA (*Carton and Giese, 2008*; *SODA, 2013*). KLIWAS are box averaged quality-controlled observations. SODA is a reanalysis of ocean climate variability of the world ocean. For the comparison, we use the following metrics through the time span 1948-2010:

1) As measure of dispersion between products we choose the Median Absolute Deviation (MAD) for being a robust (i.e., independent of the distribution) measure (*Pham-Gia and Hung, 2001*):

$$MAD = median\left(\left|Y_a - \hat{Y}\right|\right), \qquad 4.4$$

where $\hat{Y}$ are AHOI estimates and $Y_a$ and are estimates from another product.

2) As measure of the interpolation bias we use the Percentage Model Bias (PMB) based on *Allen et al. (2007)*, but multiplied by -1 to relate model overestimation to a positive PMB and underestimation to a negative one (for positive observations, as is the case for temperature and salinity):

$$PMB = 100 \cdot \frac{\sum(\hat{Y} - Y_a)}{\sum Y_a}. \qquad 4.5$$

3) As measure of interpolation skill inside the range of natural variability, we use the Model Efficiency (ME; *Allen et al., 2007*):

$$ME = 1 - \frac{\sum(Y_a - \hat{Y})^2}{\sum(Y_a - \bar{Y}_a)^2}, \qquad 4.6$$

where $\overline{Y}_a$ is the average of $Y_a$. As the deviation between $\hat{Y}$ and $Y_a$ decreases, ME increases until reaching 1 if the interpolation skill is optimal.

For the metrical comparison, and because AHOI, SODA and KLIWAS have different grids, we averaged our monthly mean temperatures and salinities, as well as those from KLIWAS, within 0.5˚ × 0.5˚ boxes centered on the SODA grid points. We tested 3 depths common to all products: 15, 25 and 70 m (for SODA they correspond to 15.02 m, 25.28 m and 70.02 m water depth). Here we discuss only the metrics at 15 m because the relative metrical relations were similar for all tested depths.

We additionally validated our results with high-frequency temperature and salinity time series from six sampling stations in the North Sea not included in AHOI (Table 4.2 and Figure 4.1). To ensure the absence of the Helgoland time series (HEL from now on), which were partly included in the BSH data, we excluded any data in a region of 0.03° around the position of these time series from our dataset.

We monthly averaged all time series and calculated the Pearson correlation and metrics described above with AHOI estimates from the corresponding nearest grid cells. To assess the loss of variability of AHOI in comparison to these higher-frequency time series, we calculated power spectra of all time series with the periodogram method (*Welch, 1967*) with time series divided into detrended 10-year segments, damped with a Hanning window and overlapping 50%.

## 4.6 Results and discussion

In the following chapters we discuss the quality of our monthly hydrographic maps and validate them with the alternative data products described above.

### *4.6.1 AHOI maps and expected errors*

Figure 4.3 to Figure 4.6 show maps of surface (0.25 m) and bottom hydrography for 1978, a year with average data amount. The evolution of these gridded maps from January to December reflects known monthly climatic changes (for instance *Janssen et al., 1999*; *Berx and Hughes, 2009*): temperature minimum in February and maximum in August; low salinity in the eastern North Sea due to the Baltic Sea outflow, strong vertical stratification in the northern North Sea and maximum horizontal temperature gradients during summer. All our monthly maps will be accessible to the scientific community in Network Common Data Form (NetCDF) from the web portal of ICES/WGOOFE.

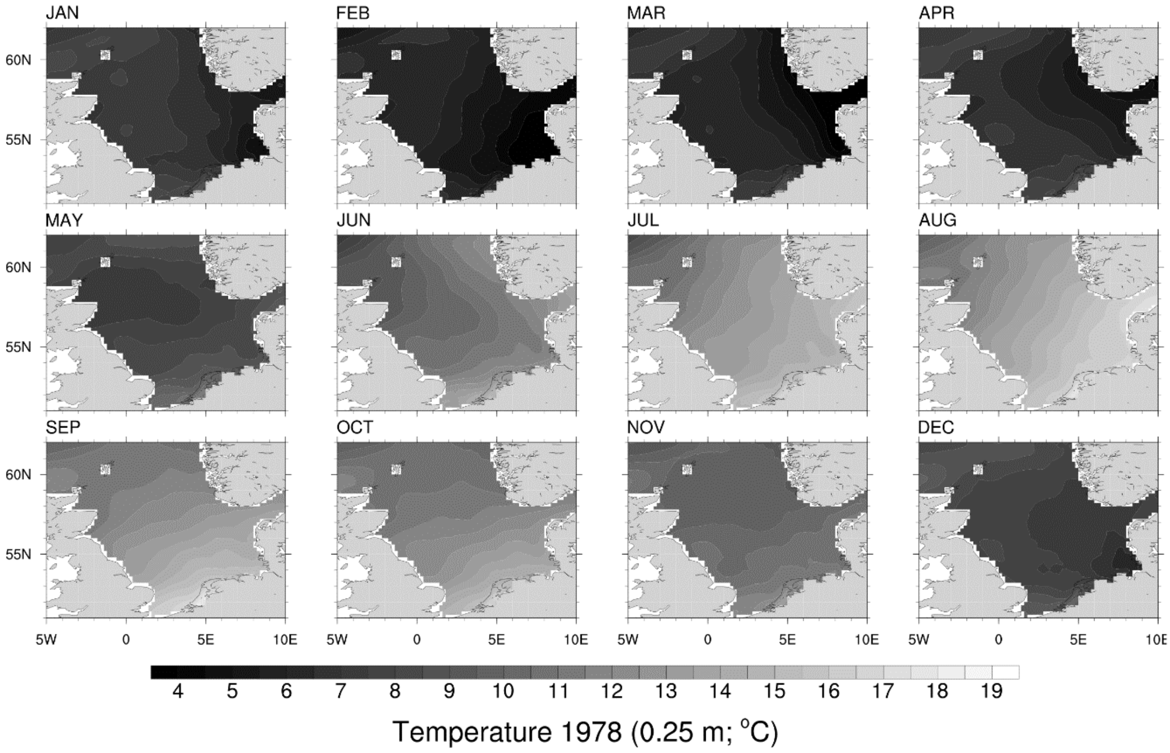

**Figure 4.3. Monthly maps of near surface (0.25 m) temperature for a year with average data amount (1978).**

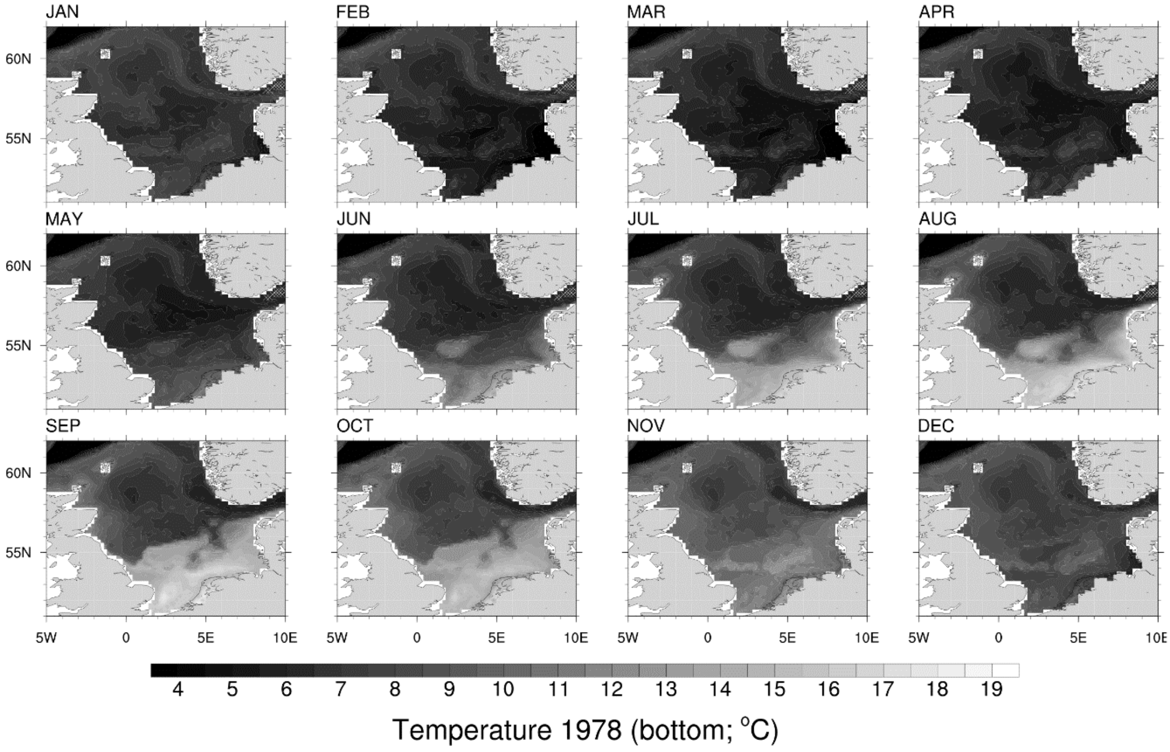

**Figure 4.4 Like Figure 4.3 but for bottom temperature.**

Our typical AHOI map represents hydrography within reasonable error limits: OI temperature errors are well below 50% of the signal variance (Chapter 4.5.4) everywhere in the North Sea all year long. Only bottom salinity shows in some regions OI errors larger than 50% of the signal variance (regions hatched in white in Figure 4.6). A discussion about the relative performances of temperature and salinity will be given in Section 4.6.5 below.

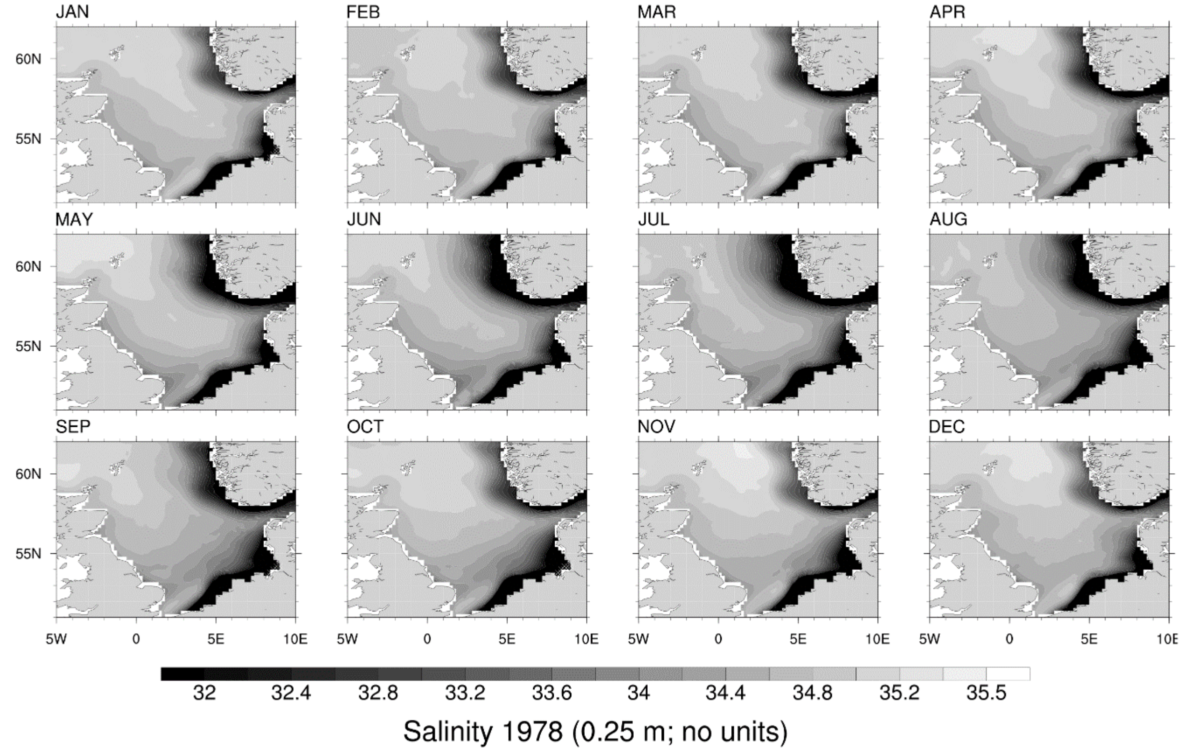

**Figure 4.5. Like Figure 4.3 but for surface salinity.**

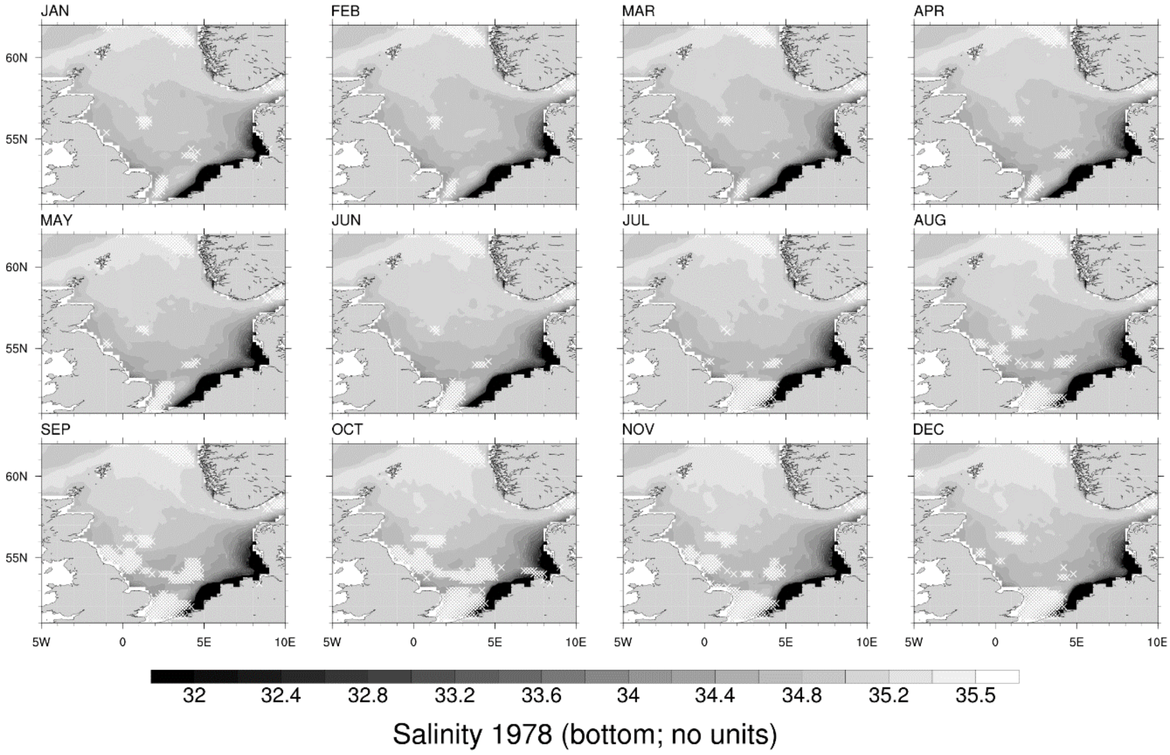

**Figure 4.6. Like Figure 4.3 but for bottom salinity. Regions where the squared OI error exceeds 50% of the signal variance (Chapter 4.5.4) are hatched in white.**

Average OI errors $\hat{E}_d$ (Eq. 4.14; Figure 4.2, panels b and e, continuous curves) are approximately 0.3°C for temperature and 0.1 for salinity at the surface, decreasing with depth. The OI errors $\hat{E}$ do not show a minimum at the depth of maximum observations (7.5 m) but monotonically decrease with depth. This suggests that $\hat{E}$ is relatively independent of the number of observations at each depth and, thus, that the data coverage in the North Sea is good (the monthly average amount of quality-controlled profiles is roughly 400). Therefore, in our particular case the observation density does not seem to be a major limiting factor of our interpolation quality.

For users interested on the individual monthly OI error maps, these are given in the NetCDF files of our data product (variables “Temperature_Error” and “Salinity_Error”). The OI expected errors roughly reflect the data distribution and indicate regions where hydrography is poorly represented for a particular month. Thus, they provide valuable information for some analyses and can, for instance, be propagated over correlation estimates, average maps, cross sections and derived variables (like density or mixed layer depth) to obtain their uncertainty. Note, however, that the OI errors are in our case not the most representative description of the accuracy of our complete analysis. These errors relate only to the accuracy of the spatial interpolation, but there are other sources of errors, like the vertical interpolation. On the contrary, the harmonic reconstruction and the adjustment for stability mostly reduce errors (Sections 4.6.5 and 4.6.7 below). Therefore, the OI error should be considered only as a rough measure of interpolation quality. Complementary and more general error estimates will be given through the metrics (Eqs. 4.4 to 4.6) in the following Sections 4.6.2 and 4.6.3.

### *4.6.2 Comparison with independent time series*

Additionally to the OI errors, we estimated alternative errors based on the reproduction of data deliberately removed at random (cross-validation). However, because profile data are often clustered, the removed data in such random cross-validation are commonly not independent of the remaining data (see for instance *Høyer and She, 2007*). In our particular case, this made the error estimates to depend on the amount of removed data. Therefore, we rejected random cross-validation as a method to estimate alternative interpolation errors. We considered instead high-frequency hydrography time series (Table 2), deliberately not included in our dataset, as alternative to validate our results: these data are sampled at fixed positions and, thus, independent of the time varying distribution of profile data.

In what follows, we compare these independent time series of temperature and salinity with AHOI time series from the mapping grid cells and depths closest to the sampling stations (Figure 4.1). We compare first the seasonal cycles as calculated from the monthly averages from the independent time series (Figure 4.7; dashed curves in dark gray areas) and their AHOI equivalents (continuous curves in light gray areas). The temperature seasonal cycle is remarkably well represented by AHOI, with overlapping standard deviations in all cases. Salinity is not so well represented, particularly for GOE and HEL, where the AHOI time series are strongly damped and show almost no changes through the year. This points out to a poor representation of salinity at the monthly time scale in regions with strong salinity gradients and high variability. The AHOI seasonal cycle is somewhat better for TER and the two STO time series because they overlap the observed ones, particularly on the second half of the year. Further, the salinity annual phase is roughly reproduced by AHOI in these three cases: STO shows minimum in the first half of the year and maximum in the second one, while TER maximum in the first half of the year and minimum in the second one.

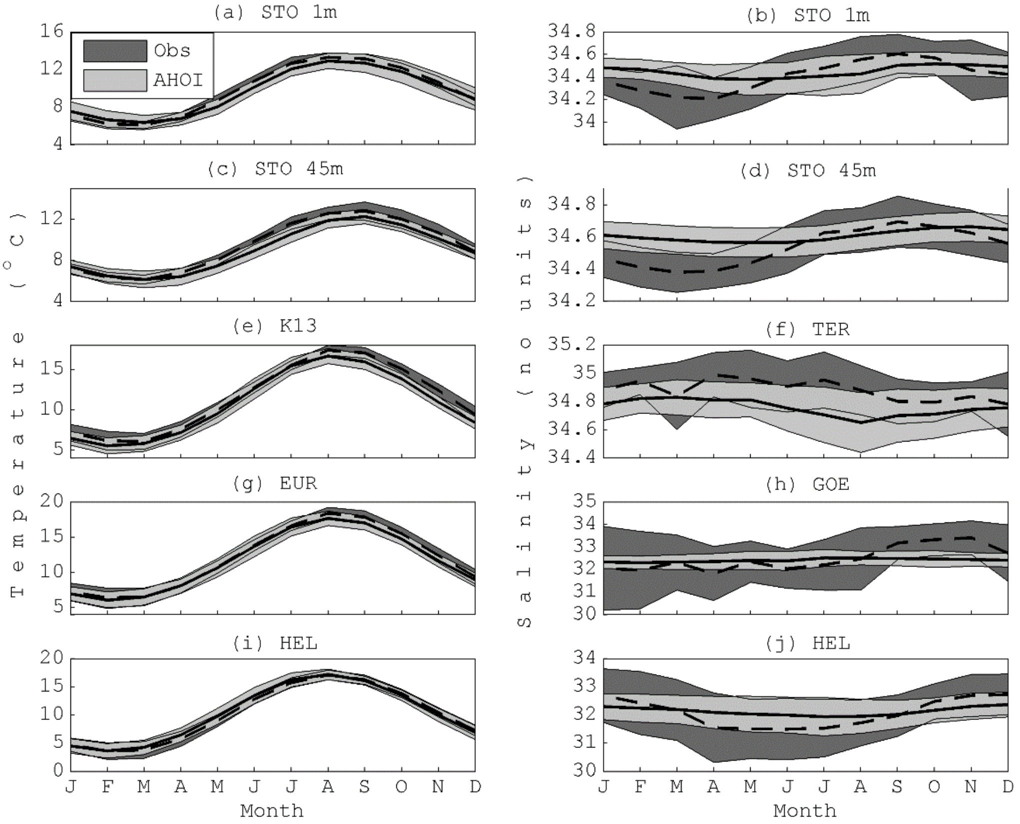

**Figure 4.7. Annual cycles of the independent time series (dashed curves; see also Table 4.2 and Figure 4.1) and their AHOI equivalents (continuous curves). Left panels: temperature; right panels: salinity. Standard deviation from the monthly average are shown with dark gray areas for the observations and with light gray areas for AHOI.**

The rough match in the STO site is encouraging because the seasonal cycle is particularly weak in the western North Sea (*Berx and Hughes, 2009*). Unfortunately, we do not have time series in the Norwegian trench region, where the salinity seasonal cycle is stronger and, thus, where a better match could be expected. Further, to our knowledge there are no previous studies where the annual cycle for salinity has been modeled for the North Sea and, thus, we cannot compare the skill of AHOI to reproduce the salinity annual cycle.

To take a closer look to the time scales represented by AHOI we compare now power spectra of the time series (Figure 4.8). Temperature power spectra (left panels) generally match well for all time series, showing major peaks at 6 and 12 months, increasing variability for periods larger than 12 months and decreasing from the semi-annual period towards the highest frequencies. The largest differences between the spectra are seen for the STO time series (see Table 4.2 for abbreviations), particularly at the surface (Figure 4.8a), where the AHOI spectrum does not reproduce correctly the bands of low variability around the annual period. This could indicate an overestimated temperature covariance length, wrongly mixing in the north-western North Sea much of the larger south-east variability. For other time series AHOI reproduces the observed variability at all frequencies fairy well.

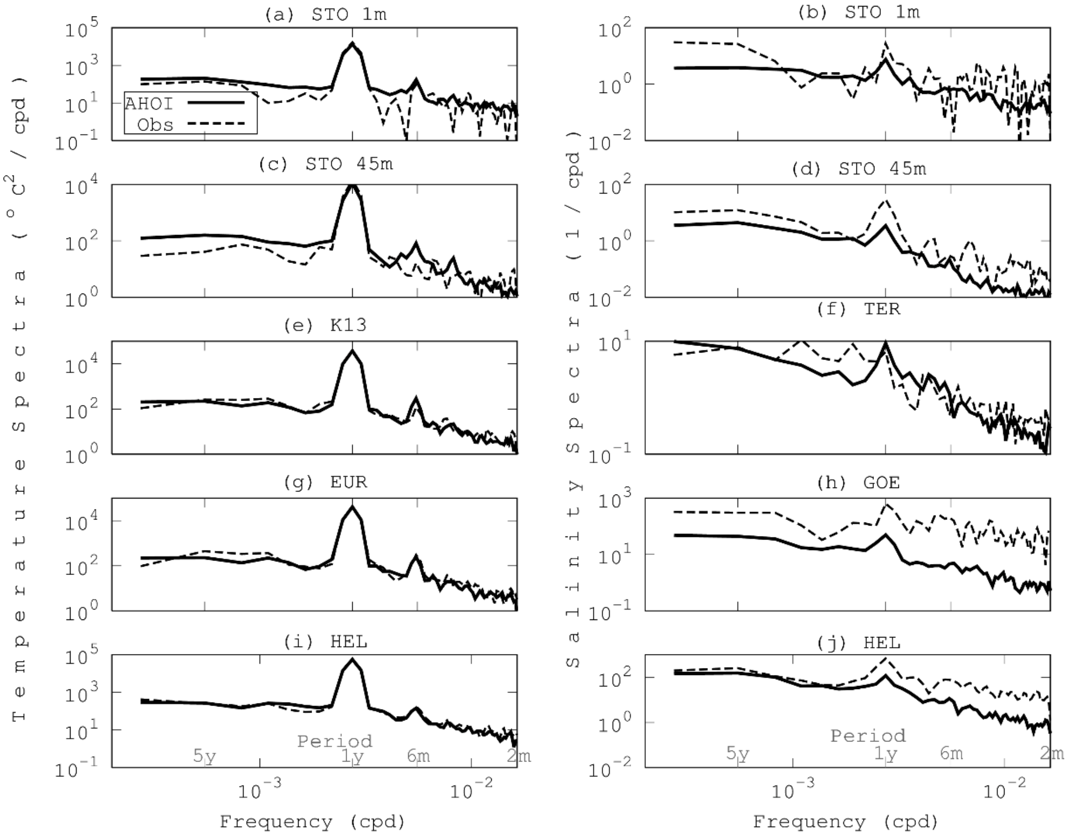

**Figure 4.8 Like Figure 4.7 but showing spectral density of the time series. Units of temperature spectra are squared degree Celsius per cycles per day (cpd) and of salinity 1/cpd. Periods in years (y) and months (m) equivalent to the frequency in cpd are shown in the x-axes in the lower panel.**

The salinity power spectra indicate that the variability of the AHOI salinity is often damped (Figure 4.8, right panels) in comparison with the independent observations. In agreement with the seasonal cycles, this damping is particularly strong in the regions of freshwater input from land (GOE and HEL, panels h and j) and at the high-frequency band (periods shorter than one year). In the extreme case of GOE, AHOI fails to reproduce the observed amount of variability showing the strongest damping at all frequencies. The comparison of power spectra is arguable because the independent time series are considerably shorter than their AHOI counterparts. However, the rough match of power spectra for periods of 6 months and larger for both variables suggests that AHOI targets rather inter-annual to inter-decadal variability at spatial scales of several kilometers. To confirm this, we calculated yearly means for each time series, filter them with a 3-year running mean (Figure 4.9) and compared them with their AHOI counterparts using the metrics described in Section 4.5.6 (Eqs. 4.4 to 4.6). An increase of temperature in the German Bight in 2002-2010 is not captured by AHOI due to lack of surface temperature observations. In spite of this and some amplitude differences (strong in surface STO), the major inter-annual oscillations of both observed and AHOI time series are in phase, comparing well statistically (Table 3): temperature MADs lie between 0.2°C in the south (HEL) and 0.6°C in the north (surface STO). *Meyer et al. (2011)* obtained a larger warm bias of roughly 0.5°C when comparing with 5-year running means of HEL (their Figure 4). The correlation between the time series is in most cases 0.8 or more, meaning a good representation of inter-annual variability for temperature. The poorest correlation was observed for EUR (0.4), but this correlation is of 0.6 without running mean (no table shown).

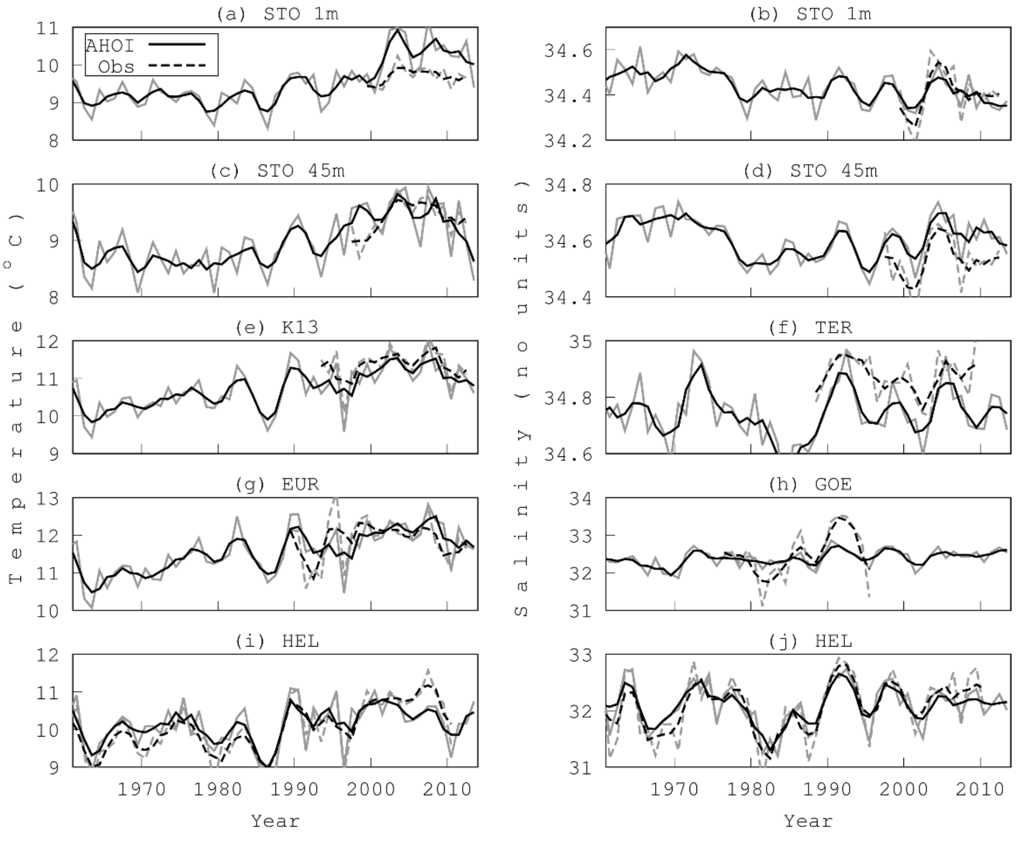

**Figure 4.9. Like Figure 4.7 but showing the corresponding time series. Grey curves are annual averages and black curves 3-year running means.**

Salinity MADs range from 0.04 salinity units for surface STO to a maximum of 0.3 for GOE. The correlation between salinity time series is in most cases equal or larger than 0.9, indicating also a good representation of salinity inter-annual variations. The exception is TER with a fair correlation of 0.7.

The ME indicates that the biases are unfortunately similar or even larger than inter-annual variations of the observed time series. Biases of the same magnitude as the natural variability seem a common shortcoming: the 0.5°C bias of *Meyer et al. (2011)* in the German Bight is comparable to the STD of temperature from HEL (approximately 0.5°C). For shorter time scales *Delhez et al. (2004)* reports errors of 70% of the natural variability for temperature and 90% for salinity in the North Sea.

Measurement inaccuracies in some of the time series cannot be ruled out as a reason for such large biases. For instance, *Hjøllo et al. (2009)* reported that the Waterbase time series (TER and GOE) are more saline than neighboring observations. A reason alternative to measurement error, in this particular case, could be an erroneously or inaccurately reported observation depth (the depth given by Waterbase is indistinctly "surface").

Therefore, we conclude for this section that the comparisons of AHOI and observed time series (Figure 4.7 to Figure 4.9 and Table 4.3) indicate that:

1. The representation of hydrography at the monthly time-scale seems limited in AHOI, particularly for salinity in the transitions zones (those with large variability). This is related to signals not only on time scales too short but also on space scales too small to be properly represented by AHOI: while the observed time series come from a single-point geographical position, their AHOI reconstructions represent an average on scales of several kilometers. GOE is a particular extreme example of this because it is in the region with the strongest salinity gradient in the North Sea (a narrow transition zone between high salinity waters from the English Channel and fresh waters from land). Thus, we recommend caution when using our salinity maps on studies related to time-scales shorter than a year.
2. Contrary to the monthly time scale, AHOI resolves inter-annual variability of temperature and salinity fairy well. Therefore our AHOI maps should be suitable for studies on the influence of various inter-annual processes, like changes of fresh water input from land and the Baltic Sea, the influence of the North Atlantic Oscillation (*Becker and Pauly, 1996*) or of large-scale circulation changes on the North Sea hydrography.

**Table 4.3. Metrics between the independent time series (abbreviations and station positions are in Table 4.2 and Figure 4.1; time series in Figure 4.9) and their AHOI equivalents, low-passed with a 3-year running mean. MAD stands for Median Absolute Difference (Eq. 4.4), "Corr" for Pearson correlation, PMB for Percentage Model Bias (Eq. 4.5) and ME for Model Efficiency (Eq. 4.6).**

| | **Time Series** | **MAD** | **Corr** | **PMB** | **ME** |
|---|---|---|---|---|---|
| **Temperature** | STO 1m | 0,6 | 0,8 | 5,8 | -15,0 |
| | STO 45m | 0,2 | 0,7 | 0,4 | -0,2 |
| | K13 | 0,3 | 0,9 | -2,4 | -0,3 |
| | EUR | 0,3 | 0,4 | 0,5 | 0,0 |
| | HEL | 0,2 | 0,9 | 0,9 | 0,7 |
| | | | | | |
| **Salinity** | STO 1m | 0,0 | 1,0 | 0,0 | 0,7 |
| | STO 45m | 0,1 | 0,9 | 0,3 | -1,4 |
| | TER | 0,1 | 0,7 | -0,3 | -5,1 |
| | GOE | 0,3 | 0,8 | -0,3 | 0,4 |
| | HEL | 0,1 | 1,0 | 0,0 | 0,8 |

### *4.6.3 Comparison with KLIWAS and SODA*

We compare now AHOI with two similar products, KLIWAS and SODA, to study how well our analysis represents the spatial distribution of hydrography at the monthly time scale. Both products use data in the North Sea similar to what we use. Therefore, this is mainly a comparison between methods, not between datasets. KLIWAS are box averaged quality-controlled observations involving neither interpolation to regions without data nor adjustment for vertical stability. Because it is related to plain despiked observations, we considered KLIWAS as the true (or signal) field of the North Sea monthly hydrography and against which to compare both AHOI and SODA.

SODA is a reanalysis of ocean climate variability of the world ocean, having to our knowledge the highest spatial resolution ($0.5^\circ \times 0.5^\circ$) and longest time span among similar products. A numerical ocean model driven by observed surface forcing is used in SODA to provide ocean state estimates, which are then corrected with observations. The ocean model compensates the lack of observations in regions with scarce data.

The temperature metrics (Section 4.5.6) between AHOI and KLIWAS (Figure 4.10, upper panels) and between SODA and KLIWAS (lower panels) indicate a closer relation of AHOI to KLIWAS in comparison to SODA: the MAD between AHOI and KLIWAS (panel a) is smaller than 0.4 °C almost everywhere except near some coastal regions, whereas SODA differs from KLIWAS more than 1°C in large regions in the central and eastern North Sea (Figure 4.10d). Both AHOI and SODA show mostly negative bias when compared to KLIWAS (Figure 4.10, b and e), but in the case of AHOI this bias is considerably smaller (also reflected by a ME closer to 1; Figure 4.10, c and f).

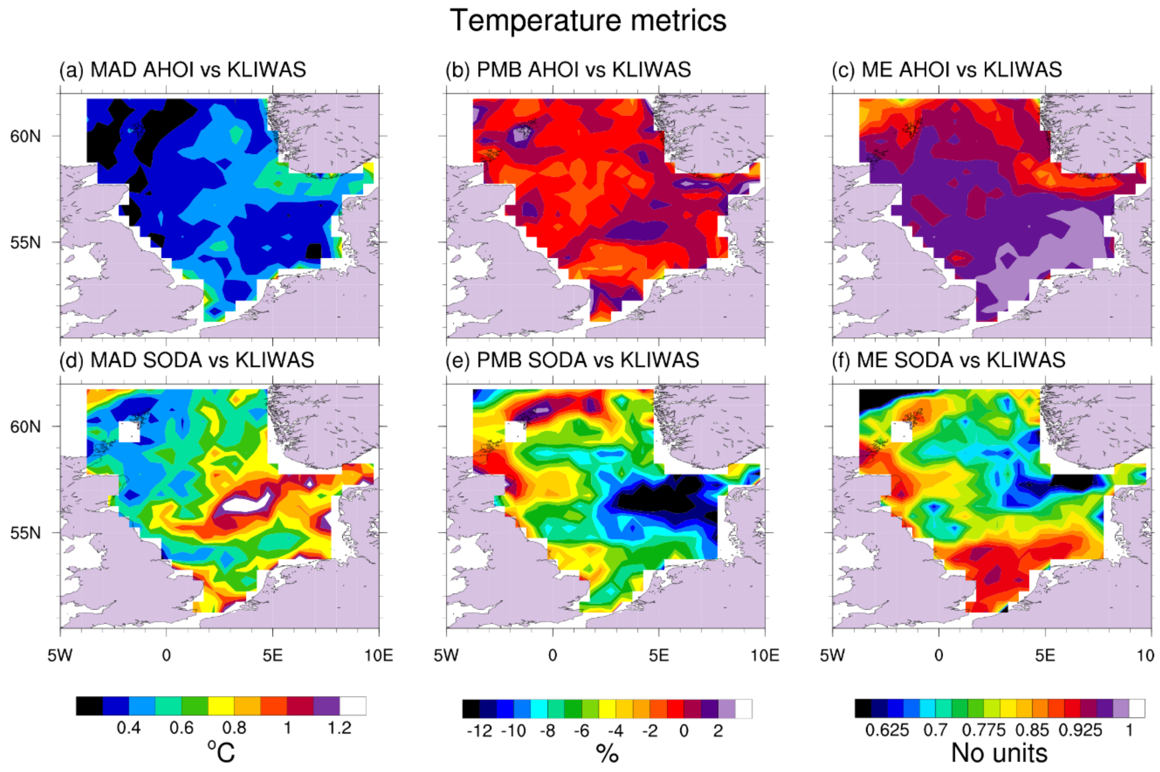

**Figure 4.10. Metrical comparison of temperature at 15 m depth between AHOI and KLIWAS (upper panels) and between SODA and KLIWAS (lower panels): Left panels: MAD (Eq. 4.4; °C); middle panels: PMB (Eq. 4.5; %); right panels: ME (Eq. 4.6; no units).**

In the case of salinity (Figure 4.11), our MAD is noticeably smaller near the coasts of Norway and continental Europe than SODA (0.45 against 0.90). SODA overestimates salinity in the freshwater regions by more than 2.5% and underestimates the inflow of high salinity water through the Strait of Dover by 1.5% (Figure 4.11e). In contrast, AHOI shows a smaller PMB of approximately 0.6% in both regions (Figure 4.11b). ME of AHOI exceeds 0.5 almost everywhere in the North Sea (Figure 4.11c), while the ME of SODA is smaller than 0.5 and even negative in the coastal regions (Figure 4.11f).

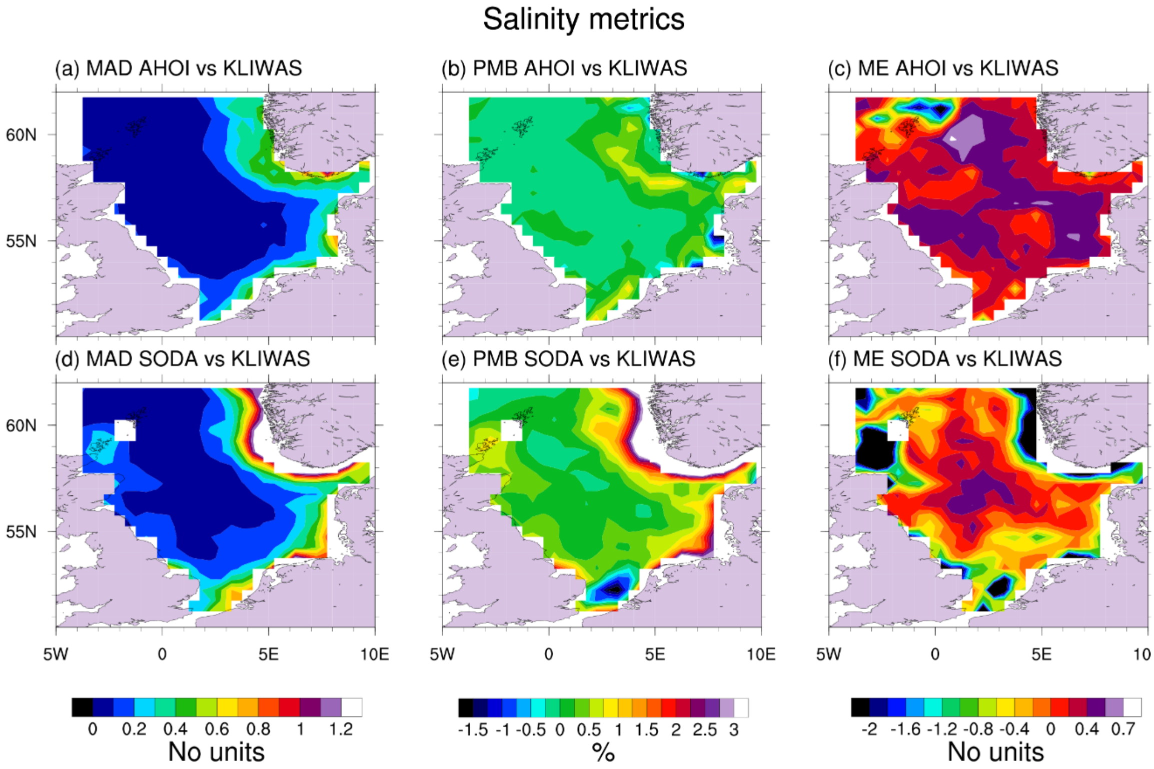

**Figure 4.11. Like Figure 4.10 but for salinity. MAD and ME are dimensionless. PMB is a percentage (%).**

Because AHOI, KLIWAS and SODA share similar data, a comparison in boxes common to all three products is a comparison in situations (i.e., regions and times) where data are available. In such situations, the metrics (Figure 4.11 and Figure 4.12) suggest that AHOI reproduces hydrography in the North Sea better than SODA. This could be explained with AHOI having an actualized observation dataset in comparison to SODA. To show that this is not the main reason, we additionally evaluated the relative performance of AHOI and SODA under situations with scarce data. We did this with a metrical comparison between SODA and AHOI in space-time boxes common to KLIWAS (Figure 4.12 and Figure 4.13, upper panels) and in space-time boxes with no KLIWAS data (lower panels). Because KLIWAS is the most comprehensive data set of the three, we can be confident that the first case represents data-rich situations and the second case data-poor situations for both SODA and AHOI. Thus, this direct comparison between SODA and AHOI is independent of the amount of data shared by both products.

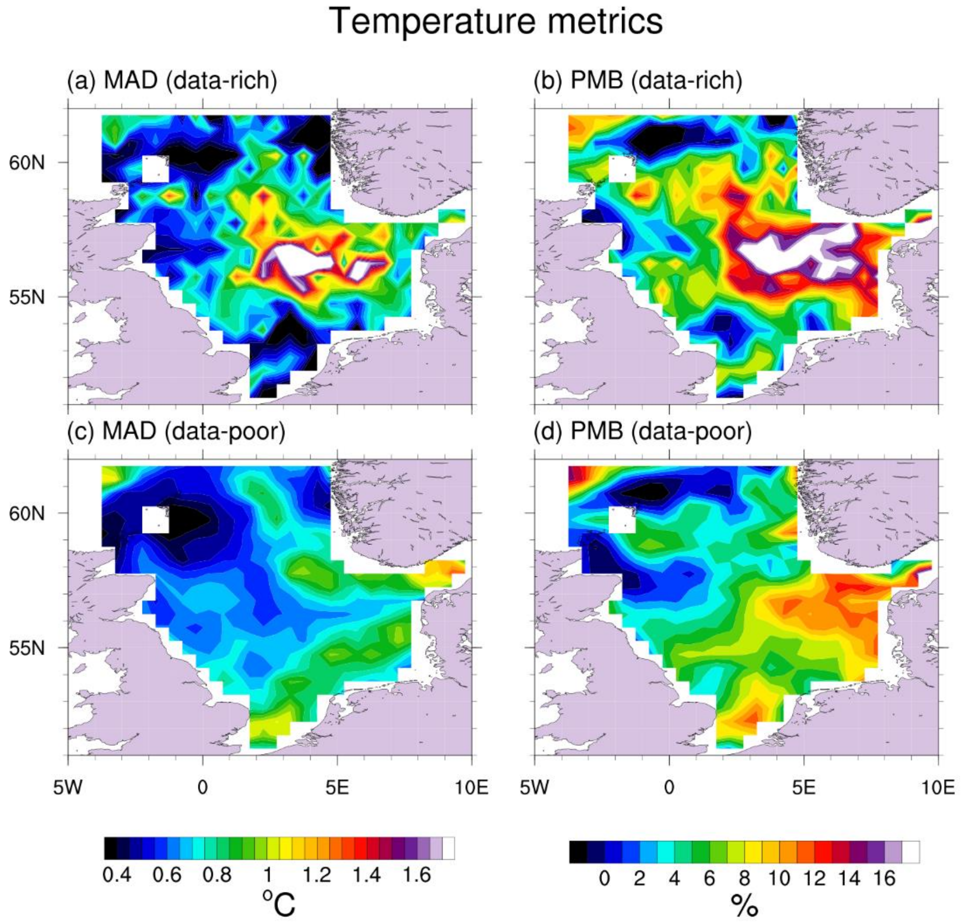

**Figure 4.12. Metrical comparison for temperature at 15 m between AHOI and SODA for data-rich situations (upper panels) and for data-poor situations (lower panels). Left panels: MAD (°C); right panels: PMB (%).**

Magnitude and geographical distribution of temperature MAD and PMB (Figure 4.12) show that AHOI is more similar to SODA in data-poor situations (panels c and d) than in data-rich situations (Figure 4.12a and b). This can mean two scenarios: 1) The skill of SODA improves in data-poor situations; 2) The skill of AHOI decreases in data-poor situations. The first case is improbable because it contradicts the foundations of data assimilation (that observations improve the model estimates). Therefore, we can conclude that the interpolation skill of AHOI for temperature in data-poor situations worsens. However, the skill of AHOI in data-poor situations does not decrease beyond the skill of SODA. This is inferred from a MAD and PMB between AHOI and SODA in data-poor situations (roughly 0.6 °C and 6%) being smaller than the metrics between SODA and KLIWAS (roughly 0.8°C and 8%). This suggests that both AHOI and SODA perform similarly in data-poor situations.

Salinity (Figure 4.13) shows similar metrics in magnitude and geographical distribution between AHOI and SODA for both data-rich and data-poor situations. This indicates that AHOI and

SODA have similar skills independently of the observation density. An explanation could be the slower-changing salinity field in comparison to temperature (reflected by a longer covariance time scale, Figure 4.16, right panels), which allows to infer salinity from previous or past months even in regions with few data.

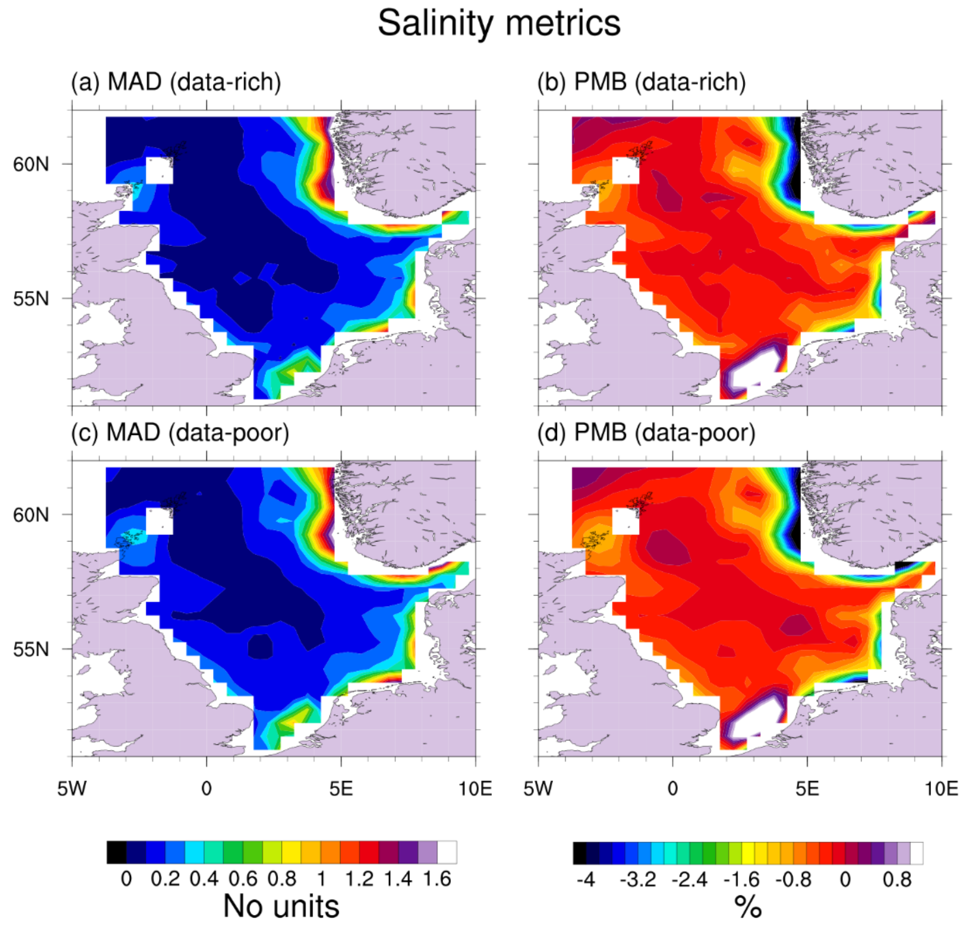

**Figure 4.13. Like Figure 4.12 but for salinity. MAD is dimensionless; PMB is a percentage (%).**

Our finding about the AHOI skill being similar to more complex global reanalysis should be considered valid only for the particular case of the North Sea and the time and space scales studied here. This should not be interpreted as if the circulation model used in ocean reanalyses negatively impacts the quality of the results. The reasons for the differences between SODA and AHOI lie probably on the low spatial resolution of SODA and on the North Sea being particular suitable for OI due to the large amounts of observations. However, to examine more carefully these reasons is beyond the scope of this study.

Again, all metrical comparisons in this section indicate that representation of hydrography in regions with large variability (coastal regions in general and the Norwegian trench for salinity) is limited at the monthly time-scale. In these regions, monthly AHOI maps should be used with care, only after an inspection of the corresponding OI error maps (Section 4.6.1 above).

### *4.6.4 Grid resolution and computational effort*

Global ocean reanalyses are to our knowledge the only source of gridded hydrography for the North Sea with reasonable estimates for both temperature and salinity and spanning the several decades needed by climate studies. Direct (non-assimilative) regional models of the North Sea have a spatial resolution similar to or better than AHOI, and could be capable of representing temperature better than global ocean reanalysis. Two examples are *Meyer et al. (2011)* (using HAMSOM with a horizontal resolution of 20 km × 20 km) and *Hjøllo et al. (2009)* (using NORWECOM with a horizontal resolution of 10 km × 10 km). However, due to the use of long-term averaged fresh water inputs (*Meyer et al., 2011*) or boundary conditions (*Hjøllo et al., 2009*) these models often fail to correctly reproduce salinity variations. This was the reason to choose an ocean reanalysis for the comparison in Section 4.6.3. There are a number of ocean reanalyses similar to SODA, for instance the MetOffice Forecast Ocean Assimilation Model (FOAM), the Hybrid Coordinate Ocean Model (HYCOM) or the second phase of the project Estimating the Circulation and Climate of the Ocean (ECCO2). However, a comparison with various products is beyond the scope of this study.

Our reconstruction demands only a fraction of the computational power needed for direct or inverse models. This allowed us to perform a large number of runs (roughly 250) and tune some of the parameters. Additionally, it enabled an unprecedented vertical resolution, leading to the accurate hydrography maps of the sea bottom needed in ecology and fisheries studies. Our analysis gains on horizontal and vertical resolution in comparison to global ocean reanalyses because its restriction to the North Sea and computational simplicity. However, Section 4.6.3 indicates that these simplifications do not imply accuracy loss in comparison to already available complex analyses.

### *4.6.5 Comparison between AHOI skills for temperature and salinity*

As we showed in previous sections, AHOI reproduces temperature better than salinity: salinity is subject to a larger OI error relative to the signal variance (Figure 4.2, b and e) and OI salinity is more undersampled or filtered in time than temperature, reproducing considerably less variability (Figure 4.7 to Figure 4.9).

The poorer interpolation skill for salinity in comparison to temperature seems independent of the method: *Delhez et al. (2004)* found also larger errors for modeled salinity than for temperature. Furthermore, both AHOI and SODA fail to reproduce correctly salinity in regions of large variability, as it is seen from the spatial distribution of their metrics (Figure 4.11). We suggest the following reasons for this:

1. There are much more temperature than salinity observations. One reason is the existence of measuring platforms intended exclusively for temperature measurement, like MBTs and XBTs, which have no salinity equivalent;
2. Salinity varies on smaller space scales than temperature due to larger measurement error, geophysical noise (high-frequency and short-range events like tides, internal waves, eddies, atmospheric low and high pressure regimes and short-term changes of river transport) and stronger horizontal gradients. This is seen in the noise-to-signal ratios (Table 4.4): The salinity noise-to-signal ratio is one order of magnitude larger than the one of temperature. This noise hinders the reproduction of the salinity field. The explanation for the different magnitudes of geophysical noise could be related to the space and time scales of their driving mechanisms: heat fluxes (which are related only to temperature changes) act on shorter time scales than processes related to both salinity and temperature (like fresh water inflows from land and precipitation, evaporation, vertical and horizontal mixing).

On average for the complete time-span, 30% of the OI salinity estimates are poor (i.e., the errors are larger than 50% of the signal variance). Such estimates are adjusted with the harmonic reconstruction based on more reliable salinity estimates from other periods (Eq. 4.3; Section 4.5.4) and, if the water column is unstable, with the stabilization routine based on temperature OI estimates (Section 4.5.5). To verify the usefulness of our harmonic reconstruction to improve poor OI salinity estimates, we calculated metrics between a harmonic reconstruction of salinity and KLIWAS from 1948 to 2010. This yielded a MAD of 0.15 and a PMB of -0.2%. These small values are not surprising because we share most of the data used in KLIWAS, which renders these metrics as measures of the residuals of the harmonic fit. However, this MAD is smaller than the salinity signal variance (approximately 0.3; Figure 4.16, lower panels), which is the best OI estimate in absence of any data. Thus, these small metrics indicate that the harmonic reconstruction fulfills its main goal of yielding a background better than the long-term climatology.

### ***4.6.6 Seasonal stratification***

In order to judge if our product is able to reproduce stratification at seasonal time scales, we compared our results with seasonal average cross-sections at 57°N from *Kangas et al. (2006)* (K06 from now on). Even if most probably sharing data with K06, this comparison is relevant for 3 reasons: 1) To further reveal possible shortcomings of our analysis; 2) To verify if our vertical resolution is enough to retain all hydrography structures observed in high resolution CTD sections; 3) To compare our skill to reproduce stratification with the skill of other products.

For the comparison we averaged AHOI data from 1980 to 1989 for the month that better matches the corresponding period of time of the K06 sections: February for winter (weeks 4-8), June for summer (weeks 24-28) and November for autumn (weeks 45-49). Our product reproduces the main seasonal features of the observed stratification fairly well (Figure 4.14). In agreement with K06 our cross-sections show a vertically mixed water column in February (panels a and b) with the 6 °C isotherm near 2.5°E and a relatively homogeneous water column over a pool of warmer bottom water (7 °C) west of it. Our thermocline at 25-30 m depth (panel c), surface fresh water layer (panel d) and near-bottom core of the cold saline Atlantic Water between 0°E and 5°E (panels c and d) compare well to the summer observations. The autumn salinity cross-sections (panel f) also match well, with the core of high salinity water at roughly 1.5 °E (though weaker in our case), slightly increasing with depth, isohalines of roughly 34.9 SU intersecting surface and bottom at 0 °E and 4 °E.

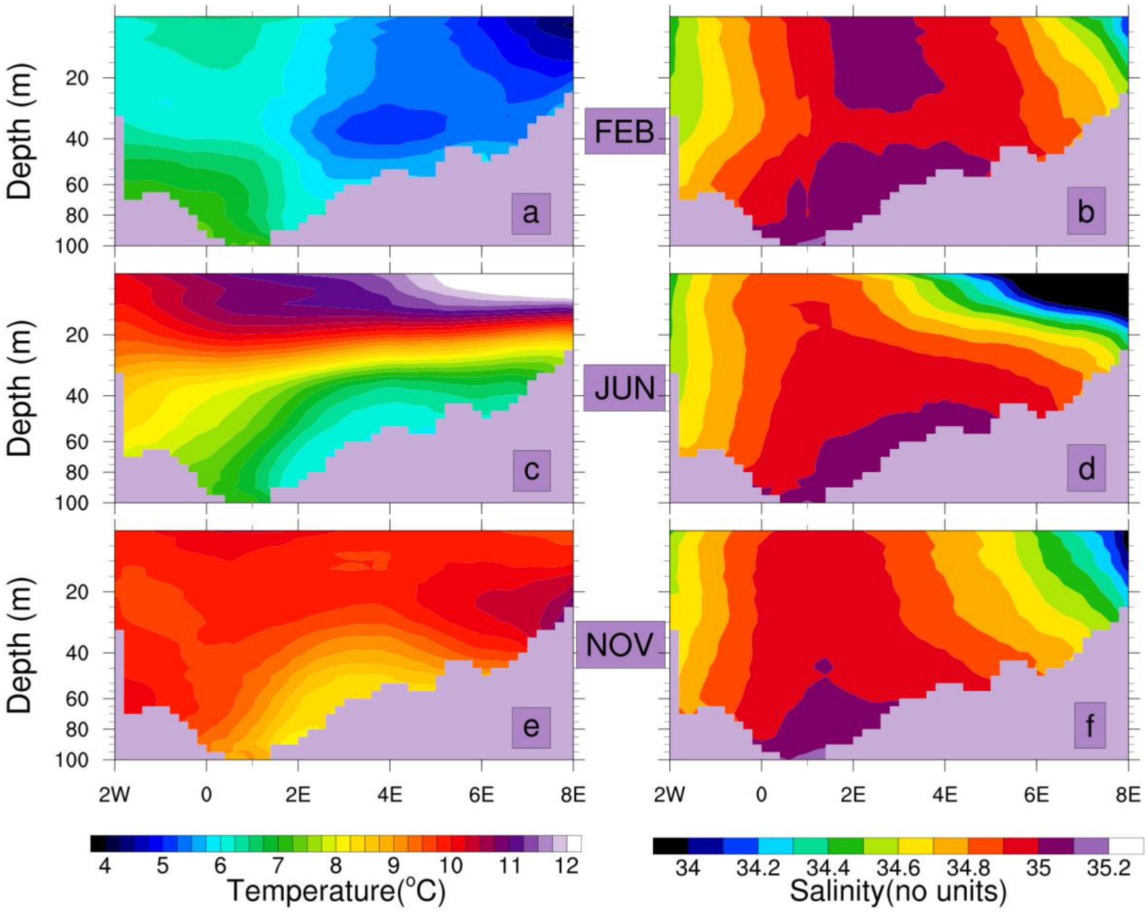

**Figure 4.14. Cross-sections of AHOI average temperature (left panels) and salinity (right panels) along the 57°N parallel for the period 1980-1999. Top panels: February (representing the K06 section for weeks 4-8); middle panels: June (representing the K06 section for weeks 24-28); bottom panels: November (representing the K06 section for weeks 45-49).**

However, there are also some differences between our sections and those of K06. Our February temperature is roughly 1 °C colder and 0.3 SU fresher at the surface eastern boundary (Figure 4.14, a and b). Most prominently, there is a temperature minimum (approximately 5 °C) near 4 °E and 40 m depth due to cold water flowing from the German Bight, which is missing in the K06 section. As consequence of this cold layer, the stability routine wrongly yields a layer of slightly (0.05 SU) fresher water at this depth, dividing the 35.0 SU salinity core in two (Figure 4.14b). However, all isohalines with salinities less than 35.0 SU reach from surface to bottom and the core of high and vertically homogeneous salinity is at similar position (roughly 2.3 °E) as in K06.

The stratification in the western region in our November temperature section is not as weak as in the case of K06. Both February and November salinity sections show fresher water (34.2 SU) in the eastern region in comparison to observations. However all the differences between our cross sections and those from K06 are inside our given accuracies of 0.3 °C and 0.1 SU, excluding those at the surface eastern boundary in November and February.

Hence our analysis reasonably represents the large-scale vertical structure of hydrography. Furthermore, the stratification patters at this section remain similar when reproduced during periods of time with no data at 57 °N (1960-1977 and 1948-1967; no figure shown). This indicates that AHOI is able of correctly reproducing seasonal stratification patterns even in the absence of direct nearby observations.

The K06 section has been also used to validate two direct models HAMSOM (*Meyer et al., 2011*) and NORWECOM (*Hjøllo et al., 2009*). The comparison with those models indicates further that AHOI represent these cross-sections within reasonable quality. For instance, *Meyer et al. (2011)* failed to correctly represent some stratification details of these sections (only for temperature; their Figure 3). Their modelled cross sections lack the core of warm bottom water in the east in both winter and autumn. In the summer section, the thermocline is broader and shallower than in K06, while the pool of bottom cold water is centered at 1 °E and not at 3° E. The reason why AHOI represents vertical stratification better than *Meyer et al. (2011)* lies probably on our enhanced vertical resolution (54 vertical layers against 19 layers in *Meyer et al. (2011)*.

*Hjøllo et al. (2009)* (their Figure 4) generally captured the seasonal variability of the stratification at the K06 section. Like in our case, there are some differences between observed and modeled temperature sections: their summer thermocline is somewhat shallower than observed, the near-bottom layer between 0 °E and 5 °E is 1 °C colder than observed. Their modeled salinity is lower in the eastern part of the section in February and November (similar to our sections). Beside this, the Atlantic water salinity core in summer is shifted too close to the British coast in comparison to observations. The visual comparison points out that our skill to reproduce the stratification in the central North Sea is similar to the one of *Hjøllo et al. (2009)*. An advance of *Hjøllo et al. (2009)* in comparison to *Meyer et al. (2011)* might lie on using bottom-following sigma layers.

In spite of coincidences and improvements, a word of caution relating our reproduction of seasonal stratification changes is needed. We could reproduce the location of the geographical location of the summer tidal front of *Holt and Umlauf (2008)* (their Figure 3) only with our August maps. In the months of June and July, where the front is present at roughly 53 °N, our stratification is still too strong to correctly represent the front at this position. These notions indicate that our product is not currently suitable for studies relating seasonal stratification changes. We need more research to understand the reasons. This, however, does not mean that AHOI also represents inter-annual stratification changes poorly (at least not if considering all data throughout the year and not only on seasonal basis). As outlook in this aspect, an OI analysis of mixed layer depth as calculated directly from the raw profiles could be more promising than studying the stratification from the interpolated fields.

### *4.6.7 Adjustment for density stability*

The last section could give the wrong impression that the adjustment for density stability negatively impacts our results in general. To show that this is seldom the case, we take a closer look to the effects of the adjustment routine in this section. Our adjustment for stability is in most regions of the North Sea a density reduction near the surface, either by increasing temperature (Figure 4.2c) or by decreasing salinity (Figure 4.2f). Comparison of KLIWAS and AHOI fields with and without vertical adjustments (no figure shown) indicates that the adjustment for stability reduces the biases in the hydrographic fields in most of the regions. There are only few small regions where the adjustment for stability increases bias by adjusting the wrong variable.

Average surface adjustments for stability are roughly 0.1°C and -0.1 salinity units and in the same order of magnitude than the average OI errors (Figure 4.2, b and e) and MADs (Table 4.3; Figure 4.10 and Figure 4.11, upper panels). We also found areas with relative strong vertical instabilities in the north-western North Sea during cold months, which coincide with the high salinity tongue of Atlantic water and where the vertical corrections were even larger. Thus, we conclude that the adjustment for density stability yield not only a physical distribution of hydrography through the water column, but was also useful to identify and reduce interpolation biases. Finally, the vertical adjustment for stability allowed visually detecting outliers by yielding strong discontinuities near the regions of measurements with unphysical values, helping to choose the outlier thresholds (Section 4.5.3).

### *4.6.8 Monthly climatologies*

As direct application of our results, we calculated monthly climatologies by time averaging individual AHOI maps, enhancing the effective resolution in comparison to previous studies.

Previous climatologies in the North Sea (*Janssen et al., 1999*; *Berx and Hughes, 2009*; *Bersch et al., 2013*) arise from averaging data first in boxes and then in time. To eliminate noise after time averaging, the resulting fields need to be filtered in space. Both box averages and space filter blend information horizontally over large spatial scales (for instance, 85 km in the case of *Berx and Hughes, 2009*) and therefore reduce the effective resolution of climatological maps. In the case of the near-bottom layer, the spatial filtering is a particular short-coming which is remedied by our approach.

OI achieves a finer spatial resolution because it uses individual observations, and not their spatial averages. Additionally, by constructing monthly climatologies from OI, we first obtain noise-free monthly maps and then average them in time. In this case no horizontal filter is needed after the time average, avoiding loss of an already enhanced resolution. Bottom maps profit from our analysis being independent for each depth level and not blending information between depths. Finally, neither *Berx and Hughes (2009)* nor *Bersch et al. (2013)* used the bathymetry gradient $|\nabla B|$ (Section 4.3) as criterion to eliminate profiles exceeding the ETOPO1 bathymetry. This could lead to a systematic profile under-sampling and thus to a poorer representation in regions with sharp bathymetry (for instance, along the edge of the Norwegian trench).

As an example of the enhanced effective resolution of our climatological maps, we show bottom temperature in Figure 4.15 (climatologies for surface temperature and surface/bottom salinity and are not shown but available in the NetCDF files). All major characteristics of the bottom temperature field from *Janssen et al. (1999)* and *Berx and Hughes (2009)* and their time evolution are present in our climatological bottom temperature: temperature minimum in February and maximum in August, when the vertical temperature stratification in the southern North Sea is minimum and the strongest temperature gradients at the bottom roughly match the 40 m isobath. Additionally, isotherms shaped by bathymetric contours are more clearly defined in our maps everywhere in the North Sea, showing structures absent or only suggested in the previous climatologies, but with finer resolution: the influence of the northern shallow plateau separating the North Sea from the Atlantic near the Shetland Islands (between 59 and 62°N) is clear all year long, with temperatures higher than in the central North Sea. The Norwegian trench edge shows a sharp gradient from September to January. The Dogger Bank and the deep channel south from it (at approximately 54°N) are clearly marked from May to November.

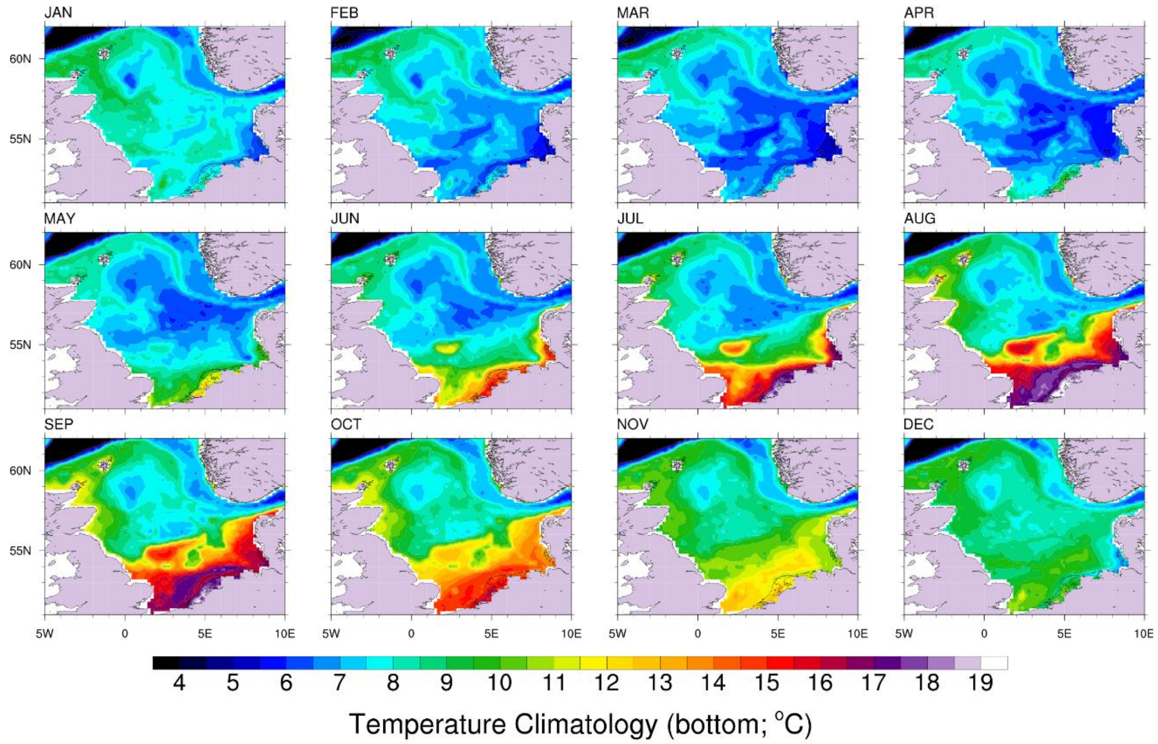

**Figure 4.15. Monthly climatology for bottom temperature.**

## 4.7 Summary and conclusions

In this study we constructed monthly maps of temperature and salinity in the North Sea through 66 years (from 1948 to 2013) by analyzing approximately 430,000 profiles and aggregated thermosalinograph data from various data bases (Table 1) with a statistical model (Adjusted Hydrography Optimal Interpolation; AHOI) mainly based on optimal (or Gauss-Markov) interpolation (OI; *Gandin, 1963*). The data were quality controlled and duplicates, outliers and vertical instabilities were removed. We estimated mean fields by fitting a running cubic surface with least squares to our data inside radii of 1.5° (approximately 165 km) for temperature and 1.0° (approximately 110 km) for salinity around each mapping point. Space-time auto-correlation functions and noise variances for temperature and salinity were estimated from our data averaged in months and boxes of 30 km x 30 km.

We mapped individual observations for each month with a resolution of 0.2° × 0.2° (approximately 20 km). Regions where the OI estimates were poor (squared error being larger than 50% of the signal variance) were replaced with a harmonic reconstruction arising from the most reliable OI estimates. This was necessary in 30% of the OI salinity estimates, but in few (less than 1%)

of the OI temperature estimates. Adjustments for vertical density stability were based on the procedures of the World Ocean Atlas (*Locarnini et al., 2010*). These adjustments yielded a physical distribution of hydrography down the water column, contributed to reduce interpolation biases and to choose the threshold for outliers (Section 4.5.3).

Possible improvements for AHOI could be using an anisotropic correlation function following the axis of the basin, an inhomogeneous variance based on the variability distribution in the North Sea or on sampling errors for each sampling platform (CTD, thermosalinograph, etc.). Most prominently, incorporating into the analysis data from heat fluxes and from river discharges should considerably improve the estimates. Our simplifications and shortcomings show as a general failure to correctly represent variations at the monthly time-scale in the regions of large variability, particularly for salinity (panels h in Figure 4.7 to Figure 4.9; Figure 4.11, a and b) but also for temperature (Figure 4.8a and Figure 4.9a), biases in some cases of the same magnitude as the natural variability (reflected by negative MEs, Table 4.3) and failure to correctly represent stratification changes (Figure 4.14, top panels). However, by analysis of OI expected errors and comparison with independent data and alternative products, we show that our results fairly reproduce variability of the North Sea hydrography on the inter-annual to decadal time scales (with temperature variability represented well even at shorter time scales).

Average OI errors are roughly 0.3 °C and 0.1 salinity units at the surface (Figure 4.2, b and e) decreasing with depth following decrement of natural variability. The accuracy of our OI through the water column seems relatively independent of the data amount (Figure 4.2, a and d), suggesting a good data coverage. Alternative error estimates (MADs) on the inter-annual time scale were obtained from the comparison with time series not included in the analysis (Table 4.2) and are on average 0.3 °C for temperature and 0.1 for salinity (Table 4.3). Correlations with these time series range from 0.4 to 0.9 for temperature and from 0.7 to 1.0 for salinity.

Salinity is, in comparison to temperature, poorly represented, which could be related to: the smaller amount of salinity observations and salinity being subject to larger measurement and geophysical noises than temperature (probably linked to the different space and times scales of the mechanisms triggering and damping temperature and salinity anomalies).

We compared our results with KLIWAS (box averaged quality-controlled observations; *Bersch et al., 2013*) and SODA (a reanalysis of ocean climate variability of the world ocean; Carton and Giese 2008; *SODA, 2013*). This comparison showed closer relations between AHOI and KLIWAS than between SODA and KLIWAS in data rich-situations (Figure 4.10 and Figure 4.11). In data-poor situations, the skill of AHOI is more similar to the skill of SODA (comparing upper and lower panels of Figure 4.12 and

Figure 4.13). These notions suggest that AHOI reproduces the spatial distribution of hydrography at the monthly scale at least with a skill similar to global ocean reanalyses. Moreover, our 66-year hydrography reconstruction demands only a fraction of the computational effort needed for direct or inverse models. This allows reproducing hydrography with a relative high horizontal and vertical resolution.

As immediate application of AHOI we have calculated new monthly climatologies of hydrography for the North Sea (Figure 4.15, for the case of bottom temperature). Our climatologies represent an improvement on effective resolution, as shown by some features of the bottom temperature field only barely visible in previous climatologies (*Janssen et al., 1999*; *Berx and Hughes, 2009*; *Bersch et al., 2013*): the northern shallow plateau near the Shetland Islands, Norwegian trench and Dogger Bank.

## 4.8 Acknowledgments

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## 4.9 Appendix: Optimal interpolation details

In this appendix we describe details relating the optimal interpolation (OI): the calculation of the quantities needed for the main OI equations (Eqs. 4.1 and 4.2), i.e., the mean fields and correlation functions, as well as the mapping grid setup and maps of OI estimates and errors. A Temperature-

Salinity diagram with all data (not shown) indicates that temperature and salinity in the North Sea are mostly independent. Therefore, all OI quantities were calculated in this study for each variable separately.

### *4.9.1 Mean fields and anomalies*

In what follows, we will denote data (both temperature and salinity) at depth level d with $Y^d$. We estimated mean fields $Y^d$ for our entire study period (1948-2013) and for each depth level d (Section 4.5.1) by fitting a running cubic surface with least squares to data near each mapping point. Only data within radii of 1.5° for temperature and 1.0° for salinity were used. To reduce biases arising from inhomogeneous data distribution over seasons, we first calculated monthly climatologies ${Y_m}^d$ and then averaged them with equal weights to produce mean fields $Y^d$. We compared our surface mean fields $Y^1$ with those of *Bersch et al. (2013)*, finding no evident differences. To obtain observation anomalies y (Eq. 4.1), we linearly interpolate mean fields $Y^d$ on the observation positions and subtract them from the observations $Y$ at each depth level $d$.

### *4.9.2 Empirical auto-covariance functions*

We used a single auto-covariance function roughly valid for all depth levels, i.e. a function arising from the vertically averaged fields $Y^v$. Using the same correlation space scales in the interpolation at each depth level should reduce vertical instabilities in the interpolated field.

To calculate anomalies for the auto-covariance function, we first bin the vertical averages $Y^v$ within time and space bins, following *Meyers et al. (1991)* and *Toompuu and Wulff (1995)*. This reduces aliasing of geophysical noise in the inhomogeneously distributed *in situ* hydrography (*Clancy, 1983*; *Meyers et al., 1991*) at scales shorter than the box size. We chose the dimensions of time and space bins of the box averages by trial and error but also based on previous studies (*Clancy, 1983*; *Meyers et al., 1991*; *Toompuu and Wulff, 1995*) and the following theoretical considerations about integral time scale (ITS) and reasonable noise-to-signal ratio.

For the time bins we chose calendar months, similar to those of *Meyers et al. (1991)* and *Toompuu and Wulff (1995)*. To justify this value in our particular case, we estimated the ITS (Eq. 5.13.16 of *Emery and Thomson, 2004*) of the temperature field. The ITS was approximately 10 days based on daily NOAA SST data with removed annual cycle. Therefore, our time bins of 30 days should filter out most of the high-frequency geophysical noise while retaining the semi-annual and lower-frequency signals.

To choose the box sizes for $Y^v$, we followed this approach: we converted positions of hydrographic stations into km by calculating zonal distances to the 2.5°E meridian and meridional distances to the 56.5°N parallel using *Vincenty (1975)* algorithm. This position was chosen for being roughly the centre of our study region. For each calendar month, the $Y^v$ values were binned within boxes of various sizes from 5 km × 5 km to 100 km × 100 km. The boxes of 30 km × 30 km were the smallest boxes yielding reasonable signal and noise variances (Section 4.9.3 below).

The box averages of $Y^v$ yield a three-dimensional data tensor ${Y^v}_{ijt}$ per variable (temperature and salinity), with index i identifying cells in the meridional direction, index j cells in the zonal direction and index t the time steps. We estimated the auto-covariance functions from this data tensor assuming that the related anomaly fields are homogeneous and stationary (*Gandin, 1963*) and that data are missing at random (*Toompuu and Wulff, 1995*). These conditions are normally not completely satisfied, but the quality of our results indicates that this cannot be critical in our case. Additionally, errors arising from failure to completely satisfy these conditions should be partially compensated by our harmonic (Section 4.5.4) and stability (Section 4.5.5) adjustments.

To obtain anomaly fields ${y^v}_{ijt}$ for the calculation of the auto-covariance function, we removed from each tensor cell ${Y^v}_{ijt}$ the time trend for every time series $(i, j)$, if less than half of the data were missing (otherwise, the time mean was removed). This approach retains the annual cycle, similar to *Meyers et al. (1991)*.

Because in our case, an anisotropic covariance function (used in *Reynolds and Smith, 1994* and *Høyer and She, 2007*) lead to poorer results, we chose a space isotropic covariance function. We first multiplied all anomalies ${y^v}_{ijt}$ with each other keeping t fixed:

$$\Pi = y^v_{ijt} \cdot y^v_{i\prime j\prime t}. \qquad 4.7$$

The cases $i' = i \wedge j' = j$ yield estimates of the variance and the cases $i' = i \vee j' = j$ of the auto-covariance for a particular time t. We repeated the process for every $t$, binning the auto-covariance estimates $\prod$ within classes $I_r$ (0 to 1100 km in 30 km intervals) of same distance r between boxes. Approximately 1×$10^4$ estimates of $\prod$ (i.e., 1×$10^4$ data pairs) were involved in each class $I_r$. We estimated expected values $e_r[\Pi]$ for the auto-covariance estimates in class $I_r$ by integrating $\prod \cdot P_r(\prod)$, where $P_r(\prod)$ is the probability density distribution for each distance class $I_r$ (estimated from the normalized histograms).

The covariance as function of time was estimated in a similar way, by multiplying anomalies ${y^v}_{ijt}$ for every time $t$, keeping $(i,j)$ fixed. All obtained empirical auto-covariance functions (dots in Figure 4.16) are well-behaved, with maximum at the origin and slowly decreasing with increasing lags.

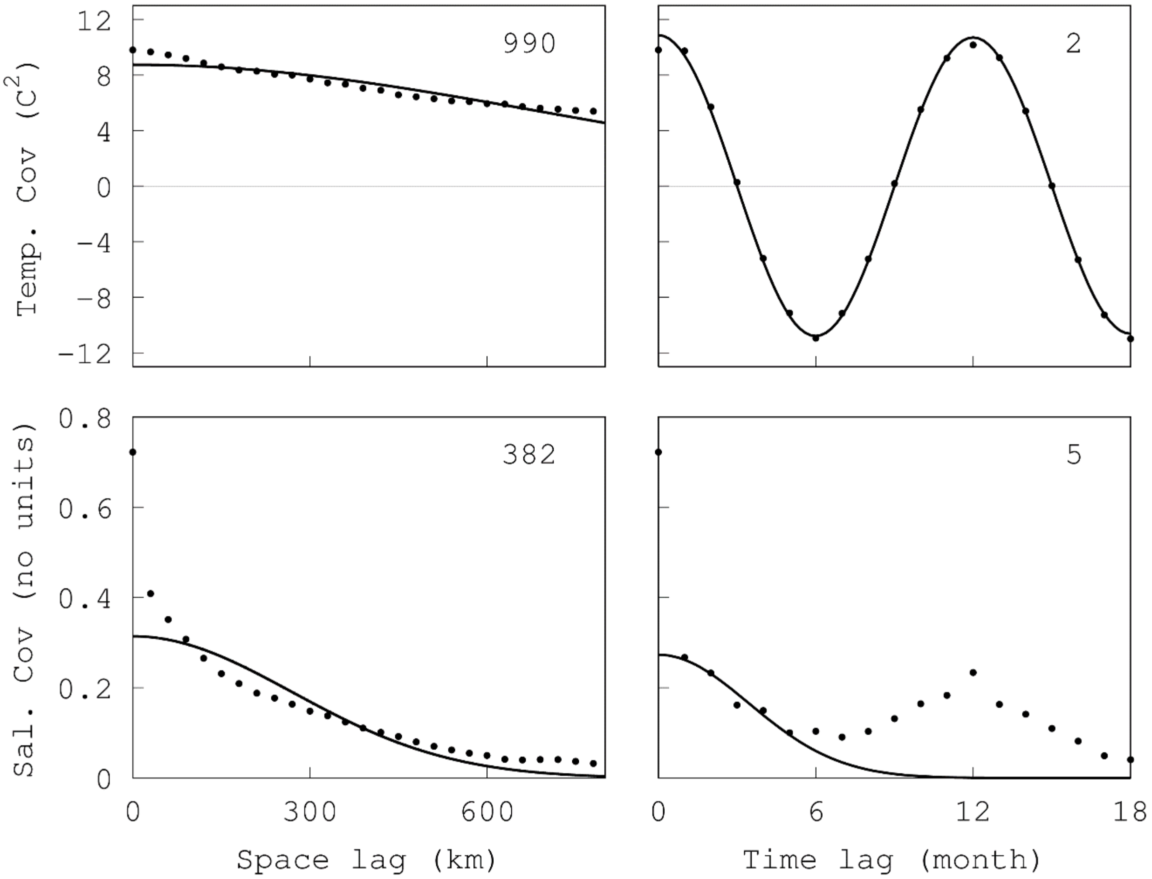

**Figure 4.16. Auto-covariance functions for vertically averaged temperature (top) and salinity (bottom) for isotropic space (left) and time (right) lags. Dots are empirical auto-covariance estimates, continuous curves are commonly used Gaussian model auto-covariances. Numbers in the upper-right corner of each panel are e-folding scales (km) and times (months).**

### *4.9.3 Model auto-correlation functions*

We modelled the empirical spatial auto-covariances with a widely used model (*Gandin, 1963*; *Clancy, 1983*; *Roemmich, 1983*; *Meyers et al., 1991*; *Reynolds and Smith, 1994*; *Høyer and She, 2007*):

$$cov(\Delta) = \sigma^2 \cdot exp\left(-\left(\frac{\Delta}{b}\right)^c\right), \tag{4.8}$$

where $\sigma$ (amplitude of the covariance function) and $b$ (e-folding scale) are parameters to be determined. $\Delta$ represents here space lags $\Delta r$ between observations in km. We chose $c = 2$ following *Clancy (1983)*, *Meyers et al. (1991)* and *Reynolds and Smith (1994)*.

To model the salinity auto-covariance as function of time we used Eq. 4.8 with time lags (i.e., $\Delta = \Delta t$) and forced the model to be zero for time lags longer than 6 months. This measure correctly reproduces the empirical auto-covariance in the first 6 months, which was otherwise not possible by fitting Eq. 4.8 without restriction. The second ridge of the empirical auto-covariance function is related to a weak annual cycle and is not represented by the model. However this does no effect our results because we do not consider time lags longer than 5 months in our analysis (Section 4.9.3 below).

To model time dependence of the temperature auto-covariance we applied an exponential model multiplied by a cosine (*Weber and Talkner, 1993*):

$$cov(\Delta t) = \sigma^2 \cdot exp\left(-\frac{\Delta t}{b}\right) \cdot cos(\gamma \cdot \Delta t), \qquad 4.9$$

where $\gamma = 2\pi/12$.

We fitted parameters $\sigma$ and b of Eqs. 4.8 and 4.9 by minimizing the quadratic differences between model and empirical auto-covariances with the downhill simplex method (*Nelder and Mead, 1965*). Noise is reflected in the empirical auto-covariance as a discontinuity at lag zero, assuming it is uncorrelated with itself and signal field (*Gandin, 1963*; *Meyers et al., 1991*). To estimate this noise, we followed *Reynolds and Smith (1994)* and fitted the model to all expected values $e_k[r]$ (dots in Figure 4.16) excluding the one at the origin. We took the difference between model and empirical auto-covariance at the origin as estimates of space (${s_r}^2$) and time (${s_t}^2$) noise variances (*Gandin, 1963*; *Julian and Thiebaux, 1975*; *Meyers et al., 1991*; *Reynolds and Smith, 1994*). In the case of the covariance of temperature as function of time, the obtained noise variance $s_t$ was negative and, thus, unphysical. We interpreted this as scales of one month being long enough to decorrelate geophysical noise in the temperature field (in agreement with the SST ITS, Section 4.9.2) and, thus have taken $s_t = 0$.

Figure 4.16 (curves) shows our modelled auto-covariance functions. To calculate single auto-correlation functions depending simultaneously on space ($\Delta r$) and time ($\Delta t$) lags, we scaled the auto-covariance functions by their signal variances $\sigma^2$ and multiply them with each other following *Reynolds and Smith (1994)* and *Høyer and She (2007)*:

$$corr(\Delta r, \Delta t) = exp\left(-\left(\frac{\Delta r}{b_r}\right)^2 - \frac{\Delta t}{b_t}\right) \cdot cos(\gamma \cdot \Delta t), \qquad 4.10$$

for temperature and

$$corr(\Delta r, \Delta t) = exp\left(-\left(\frac{\Delta r}{b_r}\right)^2 - \left(\frac{\Delta t}{b_t}\right)^2\right), \tag{4.11}$$

for salinity. $A$ and $\rho$ in Eq. 4.1 are calculated with Eqs 4.10 and 4.11. As noise-to-signal ratio s we took the sum of space ${s_r}^2$ and time ${s_t}^2$ noise variances (see for instance *Alaka and Elvander (1972)*, their Eq. 17), divided by $\sigma^2$, the average of space and time signal variances:

$$s = \frac{s_r^2+s_t^2}{\overline{\sigma}^2}. \tag{4.12}$$

Taking the average variance $\sigma^2$ as signal variance is similar to *Reynolds and Smith (1994)*. The parameters of our auto-correlation functions are shown in Table 4.4.

**Table 4.4. Parameters of the model auto-correlations for temperature and salinity (see also Figure 4.16 and Eqs. 4.10 and 4.11).**

| | Temperature | Salinity |
|---|---|---|
| Noise-to-signal ratio s | 0.1 | 2.9 |
| e-folding distance $b_r$ | 1000 km | 380 km |
| e-folding time $b_t$ | 2 months | 5 months |
| Time covariance periodicity $\gamma$ | $2*\pi/12$ | Not used |

### *4.9.4 OI maps and errors*

After eliminating outliers from the dataset (Section 4.5.3 above), mean fields, anomalies and auto-correlation functions were recalculated (Sections 4.9.1 to 4.9.3). Next, we interpolated final anomalies y (Eq. 4.1) estimated from the datasets without outliers for every depth level onto a regular spatial grid of 0.2° × 0.2° centred on the 15th day of each calendar month. We have produced like this 792 (=12 months × 66 years) monthly maps for temperature and salinity at each depth level. For each variable, maps were constructed using data inside the corresponding e-folding time (2 months for temperature, 5 for salinity; Figure 4.16) if the data did not exceed 500 observations. Otherwise, the time windows were reduced in one-day steps until the number of observations fell below 500. We chose 500 observations based on test and error as a good trade-off between computational effort and interpolation quality. Including more than 500 observations did not visibly change the OI maps.

We estimate hydrography only in the regions and depths where the mean fields were calculated (Section 4.9.1). The gridded hydrography for the ocean bottom arises from the deepest OI estimates at each grid point, provided they are above the ETOPO1 bathymetry decimated to 0.2° × 0.2° (Figure 4.1).

After mapping, we searched for OI temperature estimates lower than the freezing point (*Steele et al., 2001*) but there were no cases.

Each OI map is accompanied by a map of expected or OI errors ê (*Gandin, 1963*; *Bretherton et al., 1976*):

$$\hat{e} = \sqrt{(1 - \rho \cdot A^{-1} \cdot \rho^{T})}, \tag{4.13}$$

where $A$ and $\rho$ are calculated with Eqs. 4.10 and 4.11 and $T$ indicates transpose. The OI error $\hat{e}$ is a dimensionless quantity, ranging from 0 in regions with good data coverage to 1 in regions where data are scarce. We translate $\hat{e}$ to the corresponding units at each depth level d with:

$$\hat{E}_d = \hat{e}_d \cdot \sigma_d, \tag{4.14}$$

where $\sigma_d$ is the square root of the signal variance at each depth level ${\sigma_d}^2$ given by:

$${\sigma_d}^2 = \frac{\Sigma_d^2}{1 + s}, \tag{4.15}$$

and $\Sigma_d^2$ is the total (i.e., signal plus noise) variance at depth level d, arising from binning the quality-controlled observations in boxes (similar to the vertical mean field; Section 4.9.2). The noise-to-signal ratio s (Eq. 4.12) is assumed here to be constant with the depth.

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# 5 Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea

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## 5.1 Abstract

Understanding of the processes affecting recruitment of commercially important fish species is one of the major challenges in fisheries science. Towards this aim, we investigated the relation between North Sea hydrography (temperature and salinity) and fish stock variables (recruitment, spawning stock biomass and pre-recruitment survival index) for 9 commercially important fishes using spatially-resolved cross-correlation analysis. We used high-resolution (0.2° × 0.2°) hydrographic data fields matching the maximal temporal extent of the fish population assessments (1948-2013). Our approach allowed for the identification of regions in the North Sea where environmental variables seem to be more influential on the fish stocks, as well as the regions of a lesser or nil influence. Our results confirmed previously demonstrated negative correlations between temperature and recruitment of cod and plaice and identified regions of the strongest correlations (German Bight for plaice and north-western North Sea for cod). We also revealed a positive correlation between herring spawning stock biomass and temperature in the Orkney-Shetland area, as well as a negative correlation between sole pre-recruitment survival index and temperature in the German Bight. A strong positive correlation between sprat stock variables and salinity in the central North Sea was also found. To our knowledge the results concerning correlations between North Sea hydrography and stocks' dynamics of herring, sole and sprat are novel. The new information about spatial distribution of the correlation provides an additional help to identify mechanisms underlying these correlations. As an illustration of the utility of these results for fishery management, an example is provided that incorporates the identified environmental covariates in stock-recruitment models.

## 5.2 Introduction

Environmental conditions and fisheries are main drivers of variability of marine ecosystems (*Cushing, 1982*, *Glantz, 1992*, *Stenseth et al., 2004*). Profound responses of marine ecosystems to their changing environment have been reported all over the world at various spatial and temporal scales and trophic levels (*Martinez et al., 2009*, *Stenseth et al., 2004*, *Gladics et al., 2015*). Environmental changes are believed to trigger observed changes in abundances, composition of marine organisms and ecosystem regime shifts (*Chavez et al., 2003*, *Lees et al., 2006*, *Drinkwater, 2006*, *Beaugrand et al., 2008*). Commercially exploited fishes are an important component of fish communities in many ecosystems. Therefore our understanding of the variability of these fishes and its driving factors is not only important for optimization of the fishery management, but may also assist in predicting the effects of climate variability on whole ecosystem.

The North Sea is a complex shelf sea ecosystem, which has undergone strong changes over the last decades, mainly in zooplankton and fish communities (*Daan et al., 2005*; *Heath, 2005*; *Montero-Serra et al., 2015*). These changes are believed to be primarily driven by environmental variability and heavy exploitation of the commercial fishes (*HAWG, 2015*; *WGMIXFISH, 2015*; *ICES, 2015*). The North Sea fisheries target more than twelve commercially important species, in addition to a substantial amount of by-catch. Gadoid species, like cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*), as well as flatfish species, like plaice (*Pleuronectes platessa*) and sole (*Solea solea*), are targeted by mixed demersal fisheries. The pelagic fishery mainly targets herring (*Clupea harengus*) but also includes mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*). In addition, there is an industrial fishery for sandeel (*Ammodytes spec.*), sprat (*Sprattus sprattus*) and Norway pout (*Trisopterus esmarkii*).

Commercial stocks in the North Sea are well documented and show a high inter-annual variability in their biomass and productivity (*HAWG, 2015*, *ICES, 2015*). Together with fishing pressure this led to collapses and recoveries of the North Sea stocks, for instance, herring (e.g. *Dickey-Collas et al., 2010*) and cod (e.g. *O'Brien et al., 2000*). The reasons of the variability and collapses of many stocks are still debated and are likely to involve different mechanisms for each species.

Correlation and regression analyses have been widely used to study relations between environmental factors and stock parameters of the North Sea fish stocks (e.g. *van Der Veer and Witte, 1999*, *Planque and Frédou, 1999*, *O'Brien et al., 2000*, *Fox et al., 2000*, *Gröger et al., 2010*, *Pécuchet et al., 2014*). Previous studies dealt mainly with the influence of abiotic factors on recruitment and used various sources of information about environmental conditions in the North Sea. Some studies have used large-scale oceanic or atmospheric indexes as a proxy for local North Sea hydrography, e.g. the North Atlantic Oscillation Index (NAO; *Brander, 2005*, *Gröger et al., 2010*) or the Atlantic Multidecadal Oscillation Index (AMO; *Drinkwater, 2006*, *Brunel and Boucher, 2007*, *Alheit et al., 2014*). These studies helped to explain similarities of changes in different stocks all over the North-Atlantic by attributing them to large-scale oceanic processes. This approach might have a serious disadvantage when the link between the indices and local environmental conditions at various lags is weak (*Stenseth et al., 2003*). Furthermore, such relationships are difficult to interpret, because large-scale circulation patterns normally have a complex footprint on the local conditions and an exact mechanism behind such correlations might remain unresolved or misinterpreted.

Another group of studies exploited observations either at a particular location (*Shepherd et al., 1984*; *Rijnsdorp et al., 1992*; *Nash and Dickey-Collas, 2005*; *Sparrevohn et al., 2013*) or used various gridded products of sea surface temperature (SST; *Planque and Frédou, 1999*; *Fox et al., 2000*; *Brunel and Boucher, 2007*; *Beaugrand, 2004*). An advantage of using SST or *in situ* observations was that local temperature conditions could be addressed. But the coarse resolution of available data did not allow for analyses of spatially-resolved correlations (*Planque and Frédou, 1999*; *Livezey and Chen, 1983*). In the majority of previous studies SST data was averaged over the entire North Sea to provide a single time series for the analyses.

Recently an increasing number of studies addresses spatial heterogeneity of the North Sea and demonstrates the importance of spatial scales in the interactions between hydrography and fishes (*Hjermann et al., 2013*; *Nicolas et al., 2014*). In this study we continue in this direction by investigating the spatially-resolved influence of temperature and salinity on nine commercially important fishes in the North Sea using stock assessment data and a new reconstruction of the North Sea hydrography over the past six decades (*Núñez-Riboni and Akimova, 2015*). A high spatial and vertical resolution of the North Sea hydrography allowed for the identification of regions and depths with the strongest correlation between environmental and stock variables. A precise identification of such regions may help to identify key processes driving the variability of the fish biomass and productivity and increase the explanatory power of the environmental variables used in stock-recruitment models, as we show below.

## 5.3 Data

To study the relationships between fish stocks and environmental conditions we used a recent reconstruction of the North Sea hydrography (*Núñez-Riboni and Akimova, 2015*). This Adjusted Hydrography Optimal Interpolation (AHOI) represents monthly maps of temperature and salinity, obtained for 54 depths in the North Sea for the period from 1948 to 2013 with a horizontal resolution of 0.2˚×0.2˚. The data covers the whole North Sea from 50°N to 62°N and from 5°W to 10°E (Figure 5.1). Within the scope of this study, AHOI was further developed and improvements in comparison to (*Núñez-Riboni and Akimova, 2015*) are described in Section "The North Sea hydrography". We used here AHOI version 8.11, which is available via Figshare data portal (*Nunez, 2016*).

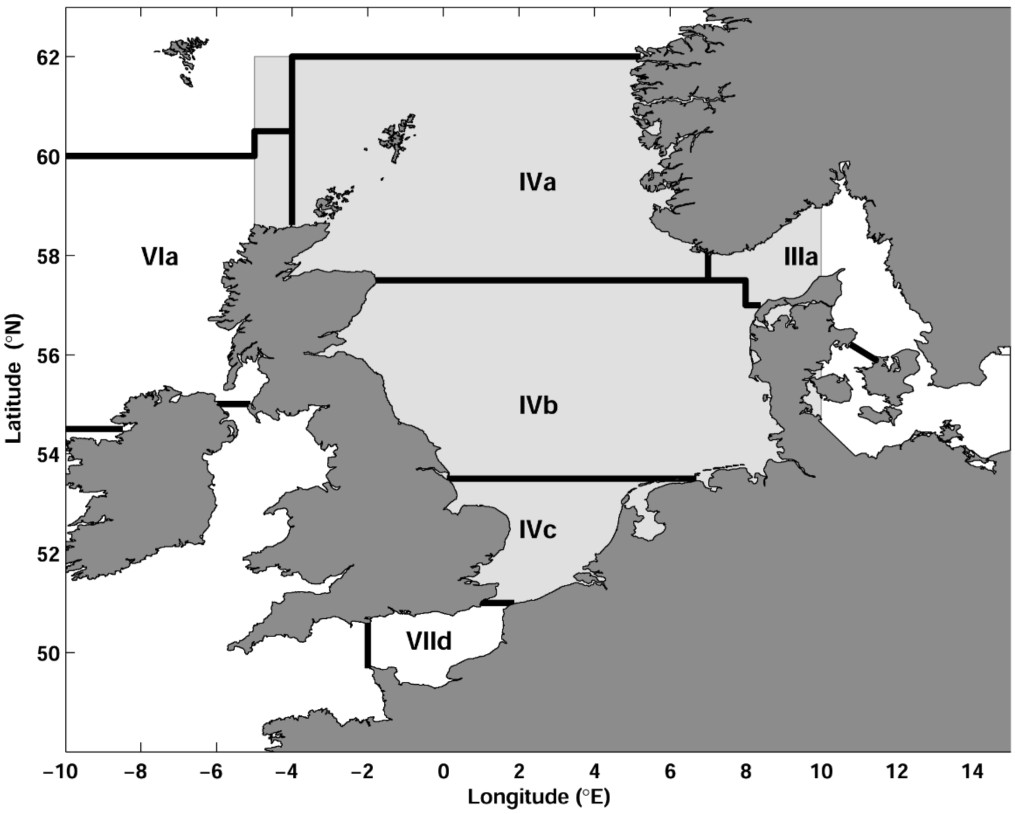

**Figure 5.1. Study area in the North Sea. The domain of AHOI (Adjusted Hydrography Optimal Interpolation) is shown in light gray. Polygons show ICES (International Council for the Exploration the Sea) stock areas for the stock assessment units used in this study (see Table 1).**

Recruitment ($R$), spawning stock biomass ($SSB$) and fishing mortality ($F$) time series of 9 assessed fish stocks in the North Sea (Table 5.1, Figure 5.1) were obtained from the database of the International Council for the Exploration the Sea (ICES; *ICES, 2015*). We used main commercially important stocks with analytical assessments (ICES category 1 assessments) with the exception of plaice and sole in Subarea VIId, because the AHOI data does not include the English Channel (Figure 5.1). We used the assessments conducted by ICES working groups in 2015 using information from catch statistics and scientific surveys (*HAWG, 2015*; *ICES, 2015*). Assessments were not downscaled if they included areas outside the North Sea (e.g., VIa or VIId in Figure 5.1) under the assumption that the main part of the stocks is distributed in ICES area IV (Figure 5.1). $SSB$ is given in tons, whereas $R$ is provided as the number of individuals and usually refers to the youngest age of the fishes caught in the fisheries or caught quantitatively in scientific surveys. The extent of the time series used in this study, as well as stock specific age of recruitment are summarized in Table 5.1. Since the AHOI dataset covers the period from 1948 to 2013 we were able to include the complete time series of stock assessment for all stocks, except herring, for which the first year of the time series (1947) was excluded from the analysis.

**Table 5.1. Fish species and their stock areas used in this study. Age at recruitment (RA) and analyzed time periods are shown.**

| Species | Stock area | RA | Time period |
|---|---|---|---|
| Atlantic cod (*Gadus morhua*) | Subarea IV, Divisions VIId and IIIa | 1 | 1963-2014 |
| Atlantic herring (*Clupea harengus*) | Subarea IV, Divisions IIIa and VIId | 0 | 1948-2013 |
| European sprat (*Sprattus sprattus*) | Subarea IV | 0 | 1974-2013 |
| European plaice (*Pleuronectes platessa*) | Subarea IV | 1 | 1957-2014 |
| Haddock (*Melanogrammus aeglefinus*) | Subarea IV, Divisions IIIa and VIa | 0 | 1972-2013 |
| Norway Pout (*Trisopterus esmarkii*) | Subarea IV and IIIa | 0 | 1983-2013 |
| whiting (*Merlangius merlangus*) | Subarea IV, Division VIId | 1 | 1990-2014 |
| common sole (*Solea Solea*) | Subarea IV | 1 | 1957- 2014 |
| saithe (*Pollachius virens*) | Subarea IV and VI, Division IIIa | 3 | 1967-2014 |

## 5.4 Methods

### *5.4.1 The North Sea Hydrography*

AHOI is based on Gauss-Markov interpolation of *in situ* observations of temperature and salinity in the North Sea (*Núñez-Riboni and Akimova, 2015*). The results of the interpolation were adjusted with harmonic analysis and with a routine for vertical density stability of the World Ocean Atlas (*Locarnini et al., 2010*). The method has been described and validated in *Núñez-Riboni and Akimova (2015)* (from now on: NRA15), where further details can be found. In comparison to NRA15, we introduced the following improvements to the North Sea AHOI dataset.

1. The time series excluded from the analysis to validate AHOI in NRA15 were included in the interpolation run used in this study (see Table 2 of NRA15).

2. In NRA15, bounds for upper and lower hydrography outliers were calculated by averaging the largest and the smallest observations inside overlapping neighborhoods around the grid points. In the present model run, these bounds were calculated by fitting a “running” cubic surface. This should better represent the outlier’s bounds near strong gradients of the mean field.

3. The adjustment for vertical stability, which was applied only to individual monthly hydrography maps in NRA15, was applied to the mean fields as well.

### 5.4.2 *Correlation Analysis*

We explored relationships between environmental conditions and stock variables by means of spatially-resolved cross-correlation analysis. We calculated the Pearson cross-correlation between stock and hydrographical time series for each grid point of AHOI at various time lags τ (*Emery and Thomson, 2004*):

$$P(\tau) = \frac{1}{\sigma_b \sigma_h} \frac{1}{N-|\tau|} \sum_{i=1}^{N-\tau} h_{i+\tau}(x, y, z) b_i, \qquad 5.1$$

where $b_i$ are anomalies of a stock variable $B$, $h_{i+\tau}(x, y, z)$ are anomalies of a hydrographical variable $H$ at time lag $\tau$ and at grid point (*x, y, z*), with latitude *x* and longitude *y* and depth *z*. $\sigma_b$ and $\sigma_h$ are standard deviations of the time series $B$ and $H$, correspondingly, and $N$ is the length of the shortest time series. The anomalies $b_i$ and $h_i$ were obtained after low-pass filtering of the original time series with a 3-year running mean and removing linear trends within the common time period. Only cross-correlations with lags $\tau$ less than 20% of $N$ were considered, following recommendations of *Emery and Thomson (2004)*.

We conducted cross-correlation analyses for 4 stock variables $B$: recruitment $R$, log-transformed recruitment $\ln(R)$, pre-recruitment survival index $R/SSB$ and spawning stock biomass $SSB$. Log-transformation of $R$ was used to linearize possible exponential relations between recruitment and environmental conditions, which have been previously reported for fish stocks in the North Sea (*Planque and Frédou, 1999*) and elsewhere (*Subbey et al., 2014*). Pre-recruitment survival index $R/SSB$ represents the amount of recruits per unit of $SSB$ and is often used in recruitment-related studies (*Hart and Reynolds, 2002*; *Aschan and Ingvaldsen, 2009*; *Heintz et al., 2013*). To calculate it, $R$ time series were shifted relative to $SSB$ time series by the age at recruitment (Table 1).

We used temperature and salinity of AHOI as hydrographical variable $H$. Marine fishes have complex life cycles (eggs, pelagic larvae, demersal or pelagic juveniles) and different life stages may respond to changes in their environment in different ways (*Rijnsdorp et al., 2009*). In order to understand which season is the most critical for the recruitment success, we tested *H* averaged over various seasons: January-March (JFM), April to June (AMJ), July to September (JAS) and October to December (OND). Yearly mean hydrography JD was tested as well.

### 5.4.3 Significance tests

The significance of obtained correlations was tested in two steps. First, we calculated confidence intervals for the cross-correlations, obtained with Eq. 1, by converting $\mathrm{P}(\tau)$ into a normally distributed variable $\mathrm{z}(\tau)$ with the Fisher transformation *Emery and Thomson (2004)*:

$$\mathrm{z}(\tau) = \frac{1}{2}(\ln(1 + \mathrm{P}(\tau)) - \ln(1 - \mathrm{P}(\tau))), \tag{5.2}$$

which has the standard error:

$$\delta_z = \frac{1}{(N^*)^{1/2}} . \tag{5.3}$$

$N^*$ is the "effective number of degrees of freedom" given by *Pyper and Peterman (1998)*:

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_{\tau=1}^{\mathrm{N}} \frac{(N-\tau)}{N} \rho_{\mathrm{h}}(\tau)\rho_{\mathrm{b}}(\tau) , \tag{5.4}$$

where $\rho_{\mathrm{h}}(\tau)$ and $\rho_{\mathrm{b}}(\tau)$ are autocorrelations at lag $\tau$ of variables *h* and *b* correspondingly. Using $N^*$ instead of the length of the time series *N* in Eq. 3 accounts for the autocorrelation of the time series in the calculation of the confidence limits of the cross-correlation $\mathrm{P}(\tau)$ (*Pyper and Peterman, 1998*; *Bonhommeau et al., 2008*; *Fox et al., 2000*; *Aschan and Ingvaldsen, 2009*). The confidence intervals of the Fisher-transformed variable $\mathrm{z}(\tau)$ were then estimated as:

$$\mathrm{z}(\tau) - z_{p/2}\delta_z < z(\tau) < z(\tau) + z_{p/2}\delta_z, \tag{5.5}$$

where $z_{p/2}$ represents the percentiles at $p/2$ of the normal distribution with zero mean and standard deviation 1. We chose p = 0.05, which corresponds to 95% confidence interval. Finally, confidence intervals for $\mathrm{z}(\tau)$ were transformed back with the inverse Fisher transformation to obtain the corresponding confidence limits for $P(\tau)$ (*Emery and Thomson, 2004*). Improving over previous studies (*Bonhommeau et al., 2008*; *Gröger et al., 2010*; *Margonski et al., 2010*), we additionally examined the confidence of the cross-correlations at negative time lags ($\tau < 0$) to verify that the chosen confidence limits effectively eliminated spurious correlations, i.e. correlations where $B$ leads $H$.

The second significance test applied here comprised field significance. The systematical search for correlations with Eq. 1 between stock variable $B$ and a large amount of hydrographical time series $H$ can inflate the chance of finding a significant correlation. If one of the hydrographic time series is significantly correlated with $B$ "by chance", the neighboring time series are likely to be significantly correlated with $B$ as well, because the hydrographical time series are spatially-correlated. Field significance tests allow determining the minimum number of $H$ time series significantly correlated with $B$ that is consistent with the spatial autocorrelation of the hydrography field. To perform field significance test we applied the approach of *Livezey and Chen (1983)*, which is based on Monte-Carlo simulations. This method has been widely used in previous studies dealing with spatiotemporal correlations (e.g. *Phillips and McGregor, 2002*; *Wu et al., 2015*; *Gulev et al., 2013*; *Hirata et al., 2013*). We chose here confidence level of 95% to match the significance level of the correlation analyses. The field significance test with this confidence level provides a number of the hydrographical time series $M_0$ that should be equaled or exceeded in our correlation analysis such that the probability of the result occurring by chance is less than 5%. For each simulation we replaced $B$ with a Gaussian-noise time series with the mean and variance identical to those of $B$. This simulated time series were then correlated with the hydrographical time series. In each simulation (400 in total) the percentage $M$ of the coefficients statistically significant with 95% confidence according to Eq. 1 was calculated. $M_0$ was estimated as 95th percentile from the histogram of $M$ and was used as a threshold for the field significance. Correlations found to be significant in the test of confidence intervals (Eq. 5), were rejected if the field significance test failed. For the fish species, where statistically significant correlation was found between environmental variables and $SSB$, we additionally tested cross-correlation between $SSB$ and fishing mortality $F$ using Eq. 1.

## 5.5 Results

Stock and environmental variables, which revealed significant correlations with 95% confidence and showed no spurious correlations at negative lags, are listed in Table 2. For these variables field significance tests were conducted. In the following sections, we present the results only for the cross-correlations, which passed both significance tests (Table 2).

**Table 5.2. Results of the field significance test for stock ($B$) and hydrographical variables ($H$), which revealed significant correlations at time lag $\tau$. The number of grid points $M_0$ (in % of the total grid points) obtained with hydrographical variables at depth of 5 m and at the bottom are shown. The subscripts of the stock variables refer to corresponding fish species (c – cod, h – herring, sp – sprat, p – plaice, ha – haddock, np – Norway pout, s – sole, sa – saithe). The subscripts of the hydrological variables refer to the season of the strongest correlation (JFM - January to March, AMJ - April to June, JAS - July to September and OND - October to December).**

| Species | $B$ | $H$ | τ | $M_0$ (5m) | $M_0$ (bottom) | Field significance test |
|---|---|---|---|---|---|---|
| cod | $R_c$ | $T_{JFM}$ | 1 | 2.97 | 6.94 | passed |
| cod | $R_c/SSB_c$ | $T_{JFM}$ | 0 | 3.08 | 8.22 | passed |
| herring | $SSB_h$ | $T_{JFM}$ | 0 | 3.53 | 4.76 | passed |
| herring | $R_h/SSB_h$ | $T_{JFM}$ | 0 | 3.44 | 5.81 | passed |
| sprat | $R_{sp}$ | $S_{OND}$ | 0 | 9.13 | 8.80 | passed |
| sprat | $SSB_{sp}$ | $S_{OND}$ | 0 | 11.26 | 9.71 | passed |
| plaice | $R_p$ | $T_{AMJ}$ | 1 | 1.02 | 8.73 | passed |
| plaice | $R_p/SSB_p$ | $T_{AMJ}$ | 0 | 3.17 | 4.89 | passed |
| haddock | $SSB_{ha}$ | $T_{JAS}$ | 0 | 5.48 | 11.81 | failed |
| haddock | $R_{ha}$ | $S_{AMJ}$ | 1 | 13.73 | 9.51 | failed |
| Norway pout | $R_{np}$ | $S_{AMJ}$ | 1 | 8.93 | 13.27 | failed |
| Norway pout | $R_{np}/SSB_{np}$ | $S_{JFM}$ | 0 | 13.40 | 11.28 | failed |
| sole | $R_s$ | $T_{AMJ}$ | 2 | 2.52 | 7.59 | passed |
| sole | $R_s/SSB_s$ | $T_{AMJ}$ | 1 | 7.01 | 11.01 | passed |
| saithe | $SSB_{sa}$ | $T_{OND}$ | 4 | 7.41 | 9.45 | failed |
| saithe | $R_{sa}$ | $S_{AMJ}$ | 3 | 8.89 | 9.94 | failed |

### *5.5.1 Atlantic Cod and Temperature*

Three variables, namely cod recruitment $R_c$, log-transformed recruitment $\ln(R_c)$ and pre-recruitment survival index $R_c/SSB_c$ showed significant negative correlations with temperature. $R_c$ and $\ln(R_c)$ were correlated with temperature at lag 1, and $R_c/SSB_c$ at lag 0 (Table 2). All three stock variables were highly correlated to each other with the coefficients between 0.74 and 0.92, therefore they showed a similar correlation with temperature. We present here the results only for $\ln(R_c)$ as being most pronounced.

Maps of correlation coefficients revealed significant correlation between $\ln(R_c)$ and temperature only in the north-western North Sea (Figure 5.2a). Regions of the significant correlation were larger at mid-depth (40-80 m), in comparison with the upper layer, where significant correlations were obtained only north-east off the Scottish coast. The correlation was significant in all quarters, but the strongest correlation was obtained with temperature in JFM. Vertically mean significant correlation in JFM was -0.63, whereas the highest absolute correlation of -0.86 was found with temperature at 75 m depth in the north-western North Sea (Figure 5.2). The correlation between temperature and $\ln(R_c)$ was strong for the whole period of observations (Figure 5.2b).

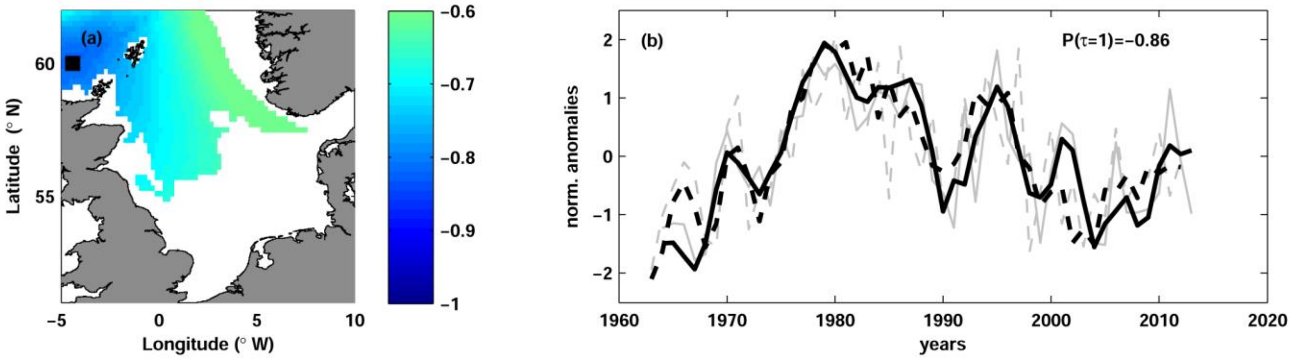

**Figure 5.2. Cod log-transformed recruitment and temperature. (a) Map of correlation between log-transformed cod recruitment $\ln(R_c)$ and temperature in JFM at lag 1 at the depth of maximal correlation (75 m). Only significant correlation is shown. The black square (60.0˚N, 4.4˚W) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $\ln(R_c)$ (dashed curves) and of water temperature (solid curves) in JFM at 75 m depth and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The temperature time series are multiplied by -1 and lagged by 1 year in order to clearly show the correlation between the time series. The correlation coefficient $P(\tau = 1)$ is shown.**

### *5.5.2 Atlantic Herring and Temperature*

We found a significant correlation between temperature at lag 0 and two stock variables of herring: negative correlation with pre-recruitment survival index $R_h/SSB_h$ and positive correlation with the spawning stock biomass $SSB_h$. The correlation between $SSB_h$ and $R_h/SSB_h$ was -0.65 and significant, whereas the correlation between $R_h$ and $R_h/SSB_h$ was weaker (0.12) and insignificant. Therefore the negative correlation between $R_h/SSB_h$ and temperature seems to be a consequence of the positive correlation between temperature and $SSB_h$. We describe here only the results for $SSB_h$.

The correlation maps showed a region of significant correlation in the north-western North Sea (Figure 5.3a). Equally strong correlations were obtained in all quarters, albeit their geographical extension varied between quarters. Only in JAS the correlation became weaker and therefore partially insignificant in the upper water layers; in other quarters the correlation was significant at all depths from the surface to the bottom. The vertically mean correlation was 0.67. The highest correlation of 0.81 was observed north-west of the Shetland Islands at 60 m depth (Figure 5.3).

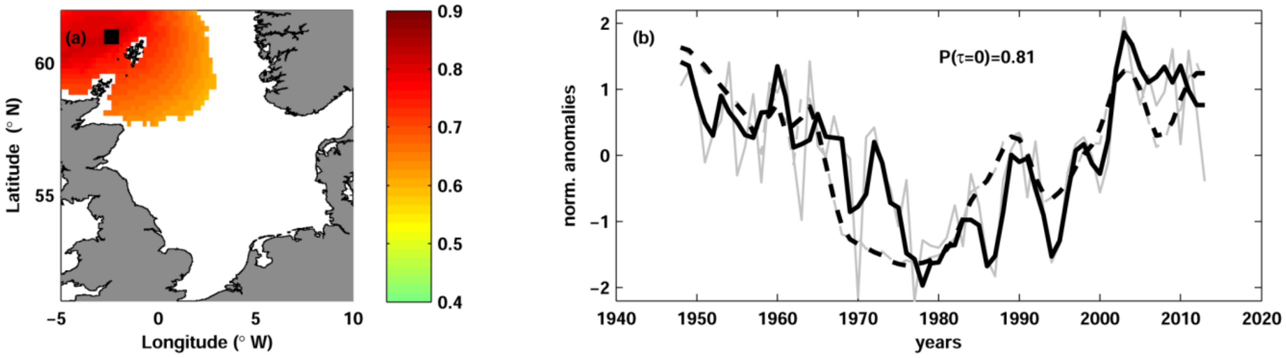

**Figure 5.3. Herring spawning stock biomass and temperature. (a) Map of correlation between herring spawning stock biomass $SSB_h$ and water temperature in JFM at lag 0 and at the depth of maximal correlation (60 m). Only significant correlation is shown. The black square (61.0 ˚N, 2.4˚W) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $SSB_h$ (dashed curves) and water temperature (solid curves) in JFM at 60 m depth and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The correlation coefficient $P(\tau = 0)$ is shown.**

Correlation between $SSB_h$ and herring fishing mortality $F_h$ was found significant at lags τ=-2, -1, 0. The strongest correlation of -0.72 was found at lag -2 (fishing mortality leads $SSB_h$ with a lag of 2 years).

### *5.5.3 European Plaice and Temperature*

Stock variables of European plaice revealed negative correlation with temperature in the North Sea. Significant correlations were found with plaice recruitment $R_p$ at lag 1 and pre-recruitment survival index $R_p/SSB_p$ at lag 0 (Table 2). Both stock variables are highly correlated with each other ($P(\tau = 1) = 0.88$) and hence show similar relations with temperature. The correlation with temperature was stronger for $R_p$ than for $R_p/SSB_p$, therefore we use $R_p$ to illustrate our results.

The correlation between $R_p$ and temperature at lag 1 was significant in the south-eastern North Sea with maximum in the German Bight (Figure 5.4a). The correlation was similar at all water depths, but slightly more pronounced at the bottom. The significant correlation was found in all quarters, except NOD, albeit its spatial extent varied slightly between quarters. The strongest correlation was found with temperature in AMJ with the vertically mean of -0.57, although it was very close to the correlation with temperature in JFM (-0.53). The highest absolute correlation value of -

0.68 was found at the bottom in the German Bight (Figure 5.4a). The correlation between $R_p$ and temperature was strong from the end of 1970s onward, whereas in the beginning of the time series the correlation was rather weak (Figure 5.4b).

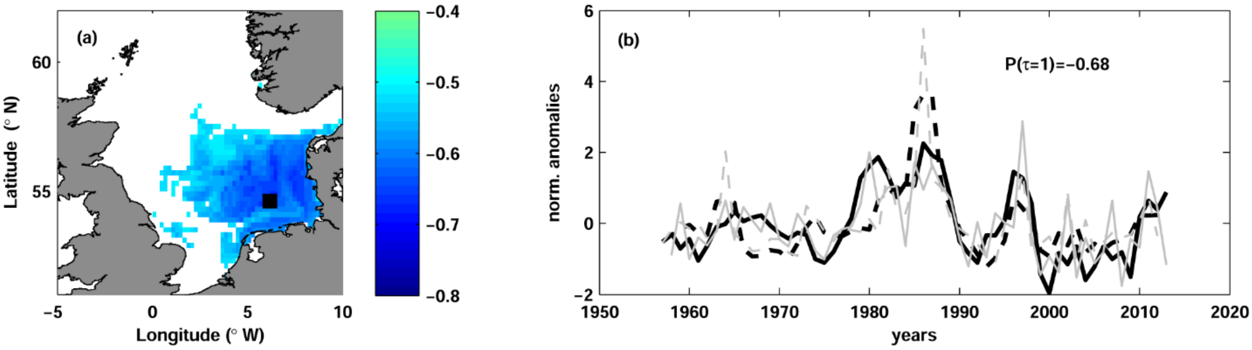

**Figure 5.4. Plaice recruitment and temperature. (a) Map of correlation between plaice recruitment $R_p$ and temperature in AMJ at lag 1 and at the depth of the maximal correlation (seabed). Only significant correlation is shown. The black square (54.8 ˚N, 5.6˚E) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $R_p$ (dashed curves) and of temperature (solid curves) in AMJ at the seabed and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The temperature time series are multiplied by -1 and lagged by 1 year in order to clearly show the correlation between the time series. The correlation coefficient $P(\tau = 1)$ is shown.**

### *5.5.4 Common Sole and Temperature*

We found negative correlations between temperature and two sole variables: sole recruitment $R_s$ at lag 2 and sole pre-recruitment survival index $R_s/SSB_s$ at lag 1 (Table 2). Both stock variables are highly correlated when the corresponding lags are taken into account ($P(\tau = 1) = 0.86$). Since the correlation with $R_s/SSB_s$ was stronger than the correlation with $R_s$, we used the first variable to describe our findings.

Similar to plaice, a region of significant negative correlation was found in the southern North Sea between 5 m depth and the bottom with the vertically mean correlation of -0.52. The strongest correlation of -0.61 was found at the bottom in the German Bight (Figure 5.5). The significant correlation was evident only in AMJ and JAS.

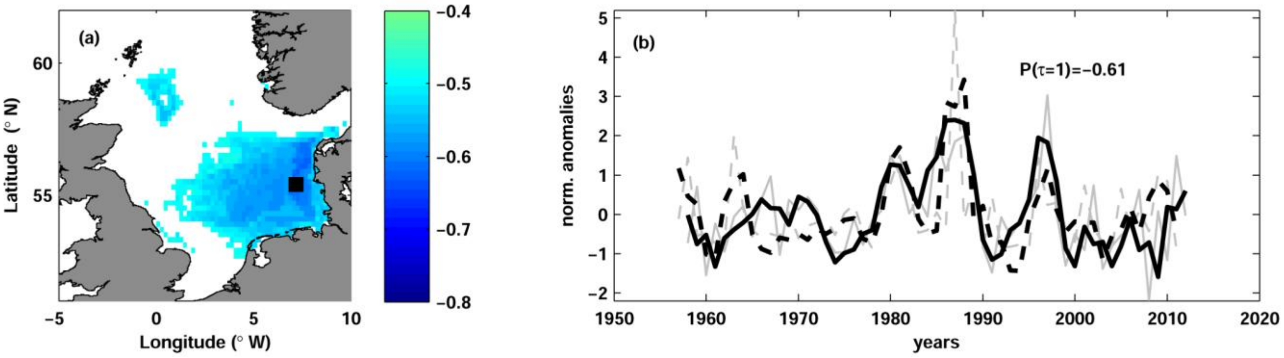

**Figure 5.5. Sole pre-recruitment survival index and temperature. (a) Map of correlation between sole pre-recruitment survival index $R_s/SSB_{ss}$ and temperature in AMJ at lag 1 and at the depth of the maximal correlation (seabed). Only significant correlation is shown. The black square (55.4 ˚N, 7.2˚E) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $R_s/SSB_s$ (dashed curves) and of temperature (solid curves) in AMJ at the seabed and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The temperature time series are multiplied by -1 and lagged by 1 year in order to clearly show the correlation between the time series. The correlation coefficient $P(\tau = 1)$ is shown.**

### *5.5.5 European Sprat and Salinity*

The time series of sprat recruitment $R_{sp}$ and spawning stock biomass $SSB_{sp}$ were found to be positively correlated with salinity at lag 0 (Table 2). The correlation maps of $SSB_{sp}$ and salinity showed significant correlations in the western North Sea along the British coast and over the Dogger Bank (Figure 5.6a), whereas the region of the significant correlation with $R_{sp}$ comprises also central and southern North Sea (Figure 5.7a). The maximal correlation was found with salinity in the upper water layer (at 20 m depth for $SSB_{sp}$ and at 10 m depth for $R_{sp}$). The correlation for both stock variables was most pronounced in OND, although significant correlations were found with salinity in other quarters as well, except JAS in the case of $SSB_{sp}$ and JFM in the case of $R_{sp}$. Vertically mean correlation with salinity in OND were 0.64 for $SSB_{sp}$ and 0.62 for $R_{sp}$. AHOI time series of salinity showing the strongest correlation with sprat $SSB_{sp}$ and $R_{sp}$ are shown in Figure 5.6b and Figure 5.7b, correspondingly.

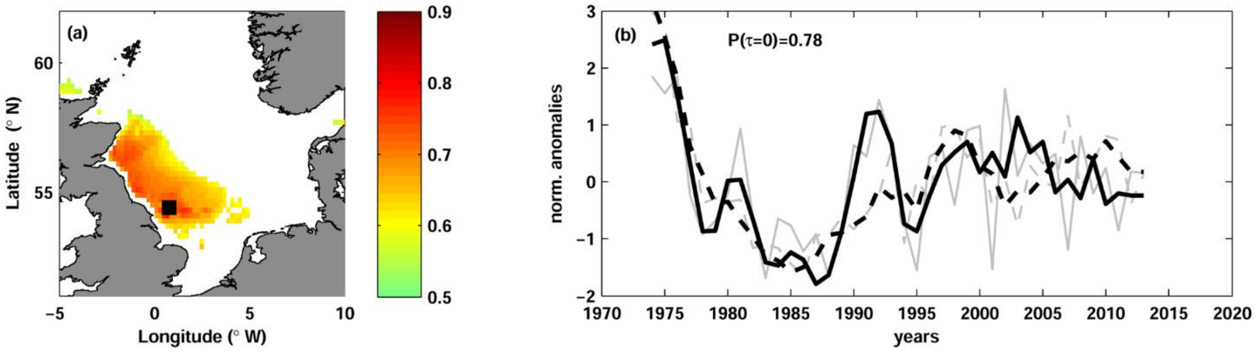

**Figure 5.6. Sprat spawning stock biomass and salinity. (a) Map of correlation between sprat spawning stock biomass $SSB_{sp}$ and salinity in OND at lag 0 and at the depth of the maximal correlation (20 m). Only significant correlation is shown. The black square (54.4 ˚N, 0.8 ˚W) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $SSB_{sp}$ (dashed curves) and salinity (solid curves) in OND at 20 m depth and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The correlation coefficient $P(\tau = 0)$ is shown.**

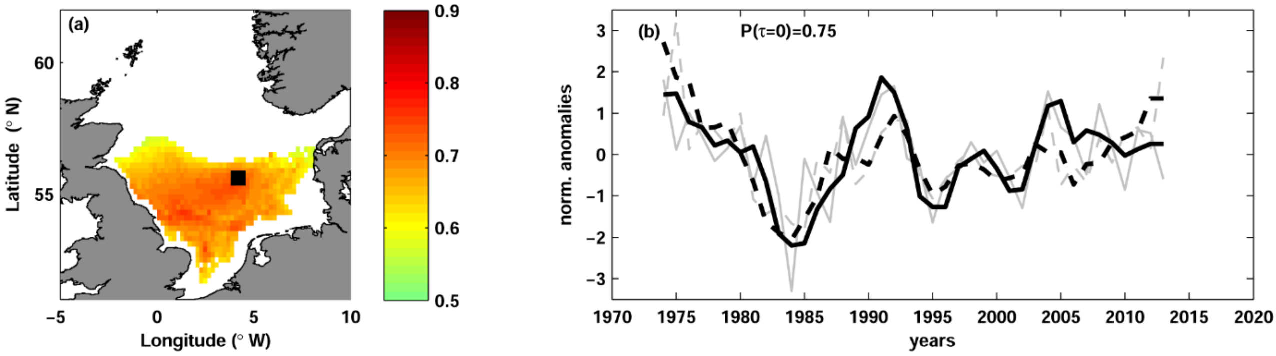

**Figure 5.7. Sprat recruitment and salinity. (a) Map of correlation between sprat recruitment $R_{sp}$ and salinity in OND at lag 0 and at the depth of the maximal correlation (10 m). Only significant correlation is shown. The black square (55.6 ˚N, 4.2 ˚E) depicts the position of the maximal correlation. (b) Time series of normalized anomalies of $R_{sp}$ (dashed curves) and salinity (solid curves) in OND at 20 m depth and at the grid point shown with the black square in panel (a). The grey thin curves show the unfiltered time series and the thick black curves are the time series low-passed with 3-year running mean. The correlation coefficient $P(\tau = 0)$ is shown.**

We tested also the correlation between $SSB_{sp}$ and sprat fishing mortality $F_{sp}$. We found a weak and insignificant correlation between these two variables at lag 0 ($P(\tau = 0)$=0.36). Correlations at other lags were also insignificant.

## 5.6 Discussion

Our study aims at improving our understanding of the linkage between climatic factors and fish stocks in the North Sea by spatially explicit cross-correlation analysis. North Sea AHOI enabled us to analyze the longest time series of stock variables so far. As mentioned in the introduction, the majority of the previous studies used mainly large scale atmospheric and temperature indices (*Gröger et al., 2010*; *Alheit et al., 2014*; *Brander, 2005*), temperature data collected parallel to the fisheries data (*Rijnsdorp et al., 1992*; *van Der Veer and Witte, 1999*) or SST averages over large areas of the North Sea (*Planque and Frédou, 1999*; *Fox et al., 2000*; *Brunel and Boucher, 2007*). All these studies missed the spatial component in their analyses. To address this gap, we studied spatially-resolved correlations between fish stocks and environmental variables in the North Sea. The goal of our study was to identify regions of the North Sea where environmental conditions seem to be more influential on stocks' variability, as well as those with little to no influence. In the previous section we showed the most relevant regions (i.e. regions of statistically significant correlation) for five fish species. To illustrate our findings we used correlation maps for depths of maximum correlation (Figure 5.2 to Figure 5.2). However, the exact depths of maximal correlations should be interpreted cautiously. Our ability to resolve spatial correlation between stock and environmental variables in the North Sea does not only depend on the spatial resolution of the available data, but is also restricted by the nature of the North Sea hydrography, i.e. by the scales of spatial (horizontal and vertical) autocorrelation of hydrographic variables. For example, temperature in the southern North Sea is highly autocorrelated vertically on the inter-annual time scales (e.g. *Lee, 1980*). Therefore obtained correlations between temperature in the German Bight and plaice recruitment are similar at all depths (maximal correlations at each depth are between -0.68 and -0.60) and are well within the correlation confidence limits. Using only correlative analyses, we cannot ascribe correlations obtained in this shallow region of the North Sea to the processes either taking place at the sea bottom or near the surface. The same is true for the European sole, e.g. the depth of maximal correlation cannot be regarded as a hint to a possible driving mechanism.

In contrast, the distribution of temperature in the northern extent of the North Sea is not vertically homogeneous. A seasonal thermocline at approximately 30m depth separates two water layers there (e.g. *Lee, 1980*). Temperature variability in these layers is driven by different mechanisms; the near-surface layer is driven mainly by the variability of the atmospheric heat fluxes, while the layer below the thermocline is driven by the temperature and strength of Atlantic Water inflow. The depth of maximal correlation obtained between herring or cod and temperature in the north-western North Sea should not be considered as exact value, but as a rough indicator of the role that near-surface or mid-depth effects might have. This will be discussed in the cases of cod and herring in the following sections.

We performed our analyses with two environmental variables (temperature and salinity) averaged quarterly without a restriction to a certain period of the year. In other words, we studied the relations between stock and hydrographic variables without presumption of a certain life-stage being the most important for the recruitment variability. This approach allowed for the identification of periods of the year having the strongest impact on the inter-annual variability of the stocks and their recruitment.

### *5.6.1 Atlantic Cod*

A negative correlation between cod recruitment and temperature has been reported previously based on the analyses of spatially averaged SST and recruitment time series (e.g., *Planque and Frédou, 1999*; *O'Brien et al., 2000*; *Olsen et al., 2011*). Various hypothesis on underlying mechanism have been proposed: match-mismatch between first-feeding larvae and zooplankton production (*Daewel et al., 2011*), temperature related changes in zooplankton community and its productivity (*Beaugrand et al., 2003*; *Nicolas et al., 2014*) and direct effects of temperature on growth and survival of cod eggs and larvae (*Otterlei et al., 1999*; *Nissling, 2014*). Beside bottom-up controls, top-down processes have been proposed, e.g. through changes in abundance of key predators (*Speirs et al., 2010*) or in the predator-prey spatial overlap (*Kempf et al., 2009*, *Kempf et al., 2013*).

Our study confirms previously reported strong negative correlation between cod recruitment and temperature in JFM (Figure 5.2). The strongest correlation was found in the north-western part of the North Sea. These results do not support the findings of (*Daewel et al., 2011*), who showed the importance of temperature in the southern North Sea for the overall recruitment success of the North Sea cod. Our analysis shows that only about 20% of the recruitment variance can be explained by the temperature variability in the southern North Sea (not shown). This compares well with almost 20% of explained variance reported in the study of *Nicolas et al. (2014)*, although direct comparison is difficult because the authors analyzed spatial and temporal variability together. In contrast to *Nicolas et al. (2014)*, the correlations with temperature in the southern North Sea found here were non-significant with our chosen significance level.

The north-western North Sea, where we found the strongest correlation, is one of the regions where Atlantic water enters the North Sea (*Lee, 1980*). The temperature there is mainly affected by local atmospheric conditions in the combination with remote temperature changes in the North Atlantic (*Becker et al., 1997*). The maximum correlation of cod recruits with temperature was found at the mid-depth (60 m) and in the region coinciding with the known distribution of Atlantic Water in the North Sea (e.g. *Lee, 1980*). Because the deeper waters are isolated from the atmospheric heat fluxes and mainly influenced by changes in temperature produced by Atlantic Water, our results indicate a particular importance of Atlantic Inflow for cod recruitment. The inter-annual temperature variations in this region and depth are around 2°C, therefore we doubt the direct influence of temperature on cod recruitment. The inflow of Atlantic Water is believed to transport zooplankton rich waters and thereby affect species composition of the zooplankton community in the North Sea (*Corten, 1999*; *Corten and Lindley, 2003*; *Reid et al., 2003*; *Beaugrand, 2004*). Our finding indirectly confirm that cod recruitment is rather influenced by the zooplankton transported with Atlantic Water (*Beaugrand et al., 2003*) than by local temperature conditions. The question remains whether cod recruitment responds to the zooplankton composition of the Atlantic Water or to the strength (i.e. volume) of the inflow.

The significant correlation in the north-western part of the North Sea may indicate that the spawning stock component from that area is most important for the overall cod recruitment, i.e. recruits stemming from this area either prevail in numbers over other spawning/nursery areas or have the strongest inter-annual variability, which overrules the variability of the recruitment success elsewhere in the North Sea. Another possible explanation is that all stock components of North Sea cod are influenced by Atlantic inflow in a similar way. However, it is difficult to decide which explanation is plausible, without having a clear division of the North Sea cod stock into sub-stocks. The scales of larval transport (*Heath et al., 2008*), juvenile dispersal and adult movements (*Wright et al., 2006*; *Wright et al., 2006*; *Righton et al., 2007*; *Neat et al., 2014*) suggest such division, but it is still under discussion (*WKNSEA, 2015*; *Nielsen et al., 2009*; *Poulsen et al., 2011*). There are numerous difficulties and uncertainties associated with the proposed sub-stocks' boundaries (see e.g., discussion in *WKNSEA, 2015*). For these reasons North Sea cod is currently assessed and managed as a single stock and only this assessment are used in our study. We suggest however that once such subdivisions are agreed, identification of main drivers of the sub-stocks' variability may substantially contribute to our understanding of the overall stock dynamics of North Sea cod.

### 5.6.2 European plaice and Common Sole

Recruitment of the European plaice showed negative correlation with temperature (Figure 5.4) in agreement with previous studies, which indicated negative correlations between temperature and year-class strength of plaice using data independent of stock assessments (e.g. pre-recruitment indices from research surveys, eggs abundances; *Bannister et al., 1974*; *Van der Veer et al., 1990* ; *van der Veer et al., 2000*). *Fox et al. (2000)* tested for correlation between temperature averaged within ICES areas and plaice recruitment, finding maximum correlations from February to June. Their results were lately confirmed by *Brunel and Boucher (2007)* with longer time series. The season of the strongest correlation of *Fox et al. (2000)* roughly agrees with our maximum correlation from April to June (Chapter 5.5.3). This time of the year corresponds to the larval and juvenile period of plaice, which is known to spawn in winter in the North Sea (*Rijnsdorp et al., 1992*, *Fox et al., 2000*).

Our results showed the strongest correlation between plaice recruitment and temperature in the German Bight, but no significant correlation in the Southern Bight or along the eastern British coast. The correlation was significant in the whole German Bight, overlapping with the plaice spawning areas there (*Hufnagl et al., 2013*), whereas plaice nursery grounds are situated mainly inshore (*Nash and Geffen, 2012*). This may indicates the importance of German Bight as spawning/nursery area for the plaice in the North Sea, although the relative contribution of different spawning areas was shown to change over time (*Hufnagl et al., 2013*).

Previous studies suggested diverse processes underlying the negative correlation between plaice recruitment and temperature. Several authors showed that the transport of the early-life stages of plaice from the spawning to the nursery areas (connectivity) is critical for the reproductive success, since the nursery areas of plaice are fixed in space (*Rijnsdorp et al., 1995*, *Hufnagl et al., 2013*). They argued that the interplay between circulation pattern and water temperature is decisive; specifically, in colder years slower development and growth rate of plaice eggs and larvae allows sufficient time to bridge the distance between plaice spawning and nursery areas before the onset of metamorphosis.

Negative correlations between fish recruitment and temperature are often associated with starvation mortality and match-mismatch mechanism during fish early-life stages (*Cushing, 1990*). Starvation mortality may be caused by a decrease of suitable prey or by a temperature increase and higher metabolic costs. In agreement with *Meyer et al. (2011)*, AHOI temperature in the southern North Sea shows a weak positive trend in the period prior to 1980s and a strong increase afterwards. Furthermore, *Rijnsdorp and van Leeuwen (1996)* showed a decrease of the growth of plaice juveniles in 1980s caused by eutrophication and beam trawling. We suggest that eutrophication could also affect food availability for plaice larvae in this period. The strong warming and changing feeding conditions might cause an onset of the food-limitation of the plaice larvae and the strengthening of the correlation between plaice recruitment and temperature since early 1980s (Figure 5.4b). A more detailed consideration of match-mismatch mechanisms for the survival of plaice larvae in the North Sea is needed to confirm or reject our suggestion.

Predation on the early-life stages was alternatively suggested to be a primary driver of the plaice reproductive successes in the North Sea. Based on findings of *Pepin (1991)*, *Van der Land (1991)* and *Fox et al. (2000)* assumed that the lower temperatures might cause a reduction of the predation pressure on plaice eggs and larvae, which would in turn enhance recruitment in cold years. However, their suggestion contradicts the study of *Nash and Geffen (2012)*, who claimed that the cumulative mortality during eggs and larval stages would increase with increasing stage duration at lower temperatures. Other sources of temperature-dependent mortality, such as embryonic malformation (*Dethlefsen et al., 1996*) or activity of pathogenic bacteria (*Fonds, 1995*) were previously suggested to underlie the negative correlation between temperature and plaice recruitment. However, these sources of mortality are generally agreed to be rather small in comparison to starvation and predation mortality, as well as mortality linked to the connectivity (*Houde, 1987*, *Peck and Hufnagl, 2012*).

Sole and plaice have similar life history and feeding preferences in the North Sea (*Teal et al., 2008*). Similar to plaice, connectivity has been shown to be important for the survival of young sole (*Lacroix et al., 2013*). But there are some important differences between both flatfishes. Sole nursery areas are restricted to the southern North Sea (German and Southern Bights; *Rijnsdorp et al., 1992*), whereas plaice nurseries are found in coastal waters throughout the North Sea (e.g. *Hufnagl et al., 2013*). Another main difference is that plaice is a temperate species, which spawns in winter in the North Sea, whereas sole is a warm-water species, which normally spawns in late spring. This difference seems to be important for the feeding conditions and offspring growth in both species (*Teal et al., 2008*).

In general, there have been many fewer studies concerning the relations between sole recruitment and environmental conditions in comparison to plaice. *Brunel and Boucher (2007)* found no significant correlation between temperature and sole recruitment at lag 0, similar to our results. *Pécuchet et al. (2014)* found temperature being significantly correlated with sole pre-recruitment survival at lag 0. They used residuals from the Ricker stock-recruitment model fitted to the observed recruitment as the pre-recruitment survival index, therefore their results are difficult to directly compare with ours. We found correlations between $R_S/SSB_S$ and temperature at lag 1 and between $R_S$ and temperature at lag 2. These lagged correlations point to a delayed response of sole recruitment to environmental changes. Such delayed response is normally ascribed to two main mechanisms (*Stenseth et al., 2004*): 1) environmental factor influences species life history 2) environmental parameter influences trophic interactions of the species (availability of suitable prey and/or relevant predators). Determination of the exact mechanism behind the lagged response of sole recruitment to temperature changes will need further investigation.

### *5.6.3 Atlantic Herring*

Atlantic herring is one of the main commercial species in the North Sea and, due to its high biomass and a "wasp-waist" trophic role, is believed to be one of the key agents of the trophic interactions (e.g. *Dickey-Collas et al., 2010*). During almost 70 years of herring stock assessment, a strong collapse in 1970s and a stock recovery from 1990s were observed (Figure 5.3). A substantial effort to understand the dynamic of this stock has been previously undertaken, mainly focusing on the dynamic of herring recruitment (*Nash and Dickey-Collas, 2005*; *Hjermann et al., 2013*; *Payne et al., 2009*; *Ottersen et al., 2013*; *Hufnagl et al., 2015*; *Corten, 2013*). We found no study about the influence of environmental changes on the biomass of adult herring in the North Sea.

Our analysis yielded a positive correlation between herring $SSB_h$ and temperature at lag 0 (Figure 5.3) and negative correlation between temperature and $R_h/SSB_h$ at the same lag (not shown). The correlation analysis of herring stock variables showed that the variability of $R_h/SSB_h$ is mainly driven by the variability of $SSB_h$ and not by the variability of $R_h$ (see Chapter 5.5.2). Therefore we believe that the correlation between herring pre-recruitment survival index $R_h/SSB_h$ and temperature is due to the correlation between $SSB_h$ and temperature and focus our discussion on the later relationship.

Although no correlation between herring spawning stock biomass and temperature has been previously reported, results of some early studies indirectly indicated such relation. *Nash and Dickey-Collas (2005)* found a positive correlation between water temperature in the northern North Sea and herring young larvae abundance index, which was in turn highly correlated with the spawning stock biomass. The biomass of *Calanus finmarchicus* (the main prey item of herring larvae) was shown to be negatively correlated with the temperature and therefore could not cause the positive correlation between larvae abundance and temperature (*Nash and Dickey-Collas, 2005*). Therefore, one can conclude that the positive correlation between larvae abundance and temperature is probably a consequence of a positive relation between spawning stock biomass and temperature. Supporting our results, *Ottersen et al. (2013)* showed that including negative temperature effect into stock-recruitment model of the North Sea herring stock significantly improves explanatory power of the model for log-transformed pre-recruitment survival index, which is consistent with our finding of the negative correlation between temperature and $R_h/SSB_h$.

The strongest correlation between herring spawning stock biomass and temperature was found in the north-western North Sea (Figure 5.3a), where two of four spawning areas are located for autumn-spawning herring (Shetland and Buchan, see for example *Heath et al., 1997*). The region between Orkney and Shetland is known as an important feeding area of adult herring (*Corten and van* *de Kamp, 1992*; *Maravelias, 1997*; *Payne, 2010*), which primary feed on zooplankton (*Calanus, Temora, Oikopleura, Amphipoda*), although fish eggs, larvae and small clupeid fishes can comprise significant portion of its diet (*De Silva, 1973*, *Last, 1987*, *Segers et al., 2007*). Tight links between herring and zooplankton distribution as well as between herring migration and zooplankton seasonal cycles have been previously shown (*Maravelias and Reid, 1995*; *Corten and Lindley, 2003*).

As we mentioned above for cod, temperature in the north-western North Sea is driven by a combination of local atmospheric conditions and remote temperature changes in the North-Atlantic. The strongest correlation between herring spawning stock and temperature was found at 60 m (Figure 5.3), i.e. in a layer relatively isolated from the atmosphere. Similar to the case of cod, this indicates that changes of herring spawning stock biomass are more strongly influenced by changes of Atlantic inflow than by the variability of the air temperature. Several mechanisms might come into play here. Enhanced temperature may directly influence the growth rate of herring and thereby cause enhanced stock biomass in warm years. However, as we mentioned, the temperature amplitudes in this region are around 2°C on the inter-annual scale, therefore we rather suggest that temperature is a proxy for other mechanisms driving variability of herring spawning stock. One likely candidate might be changes in the zooplankton composition of the Atlantic inflow and, hence, the quantity of food for adult herring. A visual comparison of herring $SSB_h$ with the time series of the zooplankton species in the North Sea (*Corten, 1999*, *Reid et al., 2003*) did not yield clear match. We hope that a detailed and accurate comparison of existing time series could shed more light on the mechanisms driving the variability of herring stock in the North Sea.

In order to understand whether herring spawning stock biomass is primarily driven by fishery or by environmental changes, we calculated cross-correlation between herring fishing mortality $F_h$ and $SSB_h$. We found the strongest correlation of -0.71 between the time series when the $F_h$ was lagged by 2 years. Therefore, the effect of fishing on $SSB_h$ seems roughly comparable to the effect of climatic changes. Additional analysis is needed to determine which factor primarily drives the variability of the herring stock in the North Sea.

### ***5.6.4 European Sprat***

Among commercially important fish species in the North Sea, European sprat is perhaps the least studied in terms of the influence of environmental conditions on its stock dynamics. From an ecological perspective, sprat is an abundant small pelagic fish species and play an important role in the trophic dynamics of marine ecosystems (*Cury et al., 2000*,*Engelhard et al., 2014*). The sprat stock in the North Sea underwent several declines during the last four decades, the most dramatically at the end of 1970s

(Figure 5.6b). Our results suggest that these declines are not caused by sprat fishery alone, because no significant correlation between sprat fishing mortality and spawning stock biomass was found (Chapter 5.5.5). As discussed within *ICES (1990)*, sprat catches decreased apparently at the same time period over a large area and, therefore, were probably caused by changing climatic conditions. The abundance and recruitment of the Baltic Sea sprat has been shown to be linked to salinity changes (*Ojaveer and Kalejs, 2009*, *Voss et al., 2011*). To our knowledge, our study illustrates for the first time a correlation between inter-annual salinity variability and sprat stock dynamics in the North Sea, although the relationships between salinity and sprat distribution has been suggested previously (*Algen and Iversen, 1980*, *Corten, 1990*).

Our analyses revealed a positive correlation between salinity and two sprat stock variables: recruitment and spawning stock biomass. Both stock variables are highly correlated with each other ($P(\tau=0)=0.72$). Since sprat is a short-lived species, the 0-group fishes are believed to comprise a significant proportion of the total biomass (*HAWG, 2015*). Therefore it is unclear whether sprat $SSB_{sp}$ drives the variability of sprat $R_{sp}$ in the North Sea or $R_{sp}$ contributes to the variability of $SSB_{sp}$. A significant correlation between salinity and sprat $SSB_{sp}$ was found in the western North Sea (Figure 5.6a). This area overlaps with known spawning areas of sprat (*ICES, 1990*, *Rogers et al., 2001*, *ICES, 2014*). The region of significant correlation with sprat $R_{sp}$ covers the whole central and southern North Sea (Figure 5.7a), coinciding with main nursery area of the North Sea sprat (*Munk, 1993*, *Baumann et al., 2009*).

Inter-annual variability of salinity in the North Sea is mainly driven by the inflow of highly saline Atlantic water in the north (*Becker et al., 1997*, *Dickson, 1971*, *Turrell et al., 1996*, *Hjøllo et al., 2009*) and river discharge from continental Europe in the south (*Schott, 1966*, *Heyen and Dippner, 1998*). A thorough study is needed to identify the primary salinity driver in the central and south-western North Sea, where the strong correlation with sprat stock variables was found. However, it seems unlikely that salinity affects the sprat distribution or growth directly, because sprat is known to tolerate a wide range of salinities and inhabits waters from the Mediterranean to the Baltic Seas (*Alheit et al., 2014*, *Whitehead et al., 1986*). We rather suggest that salinity is a tracer of other biotic or abiotic conditions that seem to be important for sprat. European sprat is strictly planktivorous during its whole life cycle (*De Silva, 1973*, *Last, 1987*, *Raab et al., 2012*), and, therefore, should be sensitive to changes in the amount/composition of zooplankton in the North Sea. As we already mentioned, Atlantic water inflow is known to affect zooplankton composition in the North Sea (*Beaugrand, 2004*, *Corten, 1999*, *Reid et al., 2003*). Rivers discharge nutrient rich waters and strongly affect water stratification in the North Sea (*Heyen and Dippner, 1998*), both are important factors influencing primary and secondary productivity. A more detailed investigation of this bottom-up control of the sprat variability is needed to discover exact mechanism behind the correlations found in our study.

### *5.6.5 Management applications*

As in many other parts of the world, commercially important fish stocks in the North Sea are managed by annual quotas, which are currently based on the Maximum Sustainable Yield (MSY) concept (*EU, 2013)*. To estimate MSY, and the associated fishing mortality and stock biomass, many aspects of the stock's biology, including the stock-recruitment relationships (SRRs) have to be taken into account and used for the projections of the future stock development. However, SRR models typically have low predictive power given that changes in the productivity of stocks can be partially driven by other factors than changes in SSB (e.g., *Gröger et al., 2010*, *Vert-pre et al., 2013*). The incorporation of environmental covariates in SRR models was shown to improve significantly their fit to historical data (e.g., North Sea cod, *Olsen et al., 2011*, *Planque et al., 2003*), and such environmental influence may be incorporated into future predictions of fish stocks as well. Fisheries management needs to be responsive to ensure a sustainable exploitation under different hydrographic regimes.

Our study supports the notion of profound influence of climate forcing on stock dynamics of 5 commercially important fishes in the North Sea. Some of the correlations found in this study have been shown previously, but we were able to increase the explanatory power of the environmental covariates by identifying regions of strongest correlation. As one of many possible approaches for including such relationships in management, we propose that time series of temperature and salinity in the regions of maximum correlations may be further used in SRR models that take into account environmental effects in different ways (e.g., *Cook and Heath, 2005*). The best model for each fish species can be chosen based on the Akaike Information Criterion (AIC, *Akaike, 1974*) or cross-validation and can provide insight into the possible influences of environmental factors to fish stocks. For example, environmental factors may control the stock through mortality rates, or limit it by altering the carrying capacity, etc. (see *Iles and Beverton, 1998*). Such an approach is (at least partially) mechanistic and should be most effective for management (*Punt et al., 2013*).

As an example, we show how this approach might be applied to North Sea cod. We followed the methodology of *Levi et al. (2003)*, whereby various types of SRRs were fitted to historical data, some of which were modified to incorporate differing types of environmental effects (e.g. “limiting”, “controlling” and “masking” effects). Fitting was performed using a non-linear least squares approach with log-transformed versions of each model (Table 3). The temperature time series that best correlated to recruitment dynamics (Figure 5.2b) was used as the environmental covariate. Both AIC and cross-validation statistics showed significant improvements in fit for models that incorporated environmental effects, with a Cushing-type model incorporating “environmental masking” as the best overall (Table 3).

**Table 5.3 Summary statistics for fitted SRR model to historic data on spawning stock biomass (SSB) and recruitment (R) of the North Sea cod used in this study. *E* represents the environmental variable (in this particular case, temperature anomalies at 60.0˚N, 4.4˚W at 75 m depth; Figure 5.2), a, b, c, α, β, γ are fitted coefficients. AIC is Akaike information criterion, $R^2$ is R-squared (log-transformed recruitment); RMSE is root-mean-square error (log-transformed recruitment) and MdAPE is median-absolute-percent error (recruitment). * indicates statistics calculated from a 4-fold cross-validation procedure (50 permutations). Numbers in parenthesis indicate rankings of the top three performing models for each statistic.**

| SRR type | Env. effect | Formula (R=…) | AIC | $R^2$ | RMSE* | MdAPE* |
|---|---|---|---|---|---|---|
| Cushing | none | $\alpha\mathrm{SSB}^{\gamma}$ | 96.2 | 0.505 | 45.10 | 0.608 |
| | Controlling | $\alpha\mathrm{SSB}^{\gamma}\mathrm{e}^{\mathrm{c}E}$ | (3) 76.5 | (3) 0.676 | (3) 35.65 | (2) 0.508 |
| | Masking | $\alpha\mathrm{SSB}^{\gamma+\mathrm{c}E}$ | (1) 76.3 | (1) 0.678 | (1) 35.36 | (1) 0.506 |
| Beverton-Holt | none | $\mathrm{SSB}/(\mathrm{b}+\mathrm{aSSB})$ | 97.4 | 0.496 | 45.06 | 0.620 |
| | Controlling | $\mathrm{SSBe}^{\mathrm{c}E}/(\mathrm{b}+\mathrm{aSSB})$ | 76.6 | 0.676 | 35.81 | 0.509 |
| | Masking | $\mathrm{SSB}/(\mathrm{be}^{\mathrm{c}E}+\mathrm{aSSB})$ | 78.3 | 0.665 | 37.36 | 0.512 |
| | Limiting | $\mathrm{SSB}/(\mathrm{b}+\mathrm{ae}^{\mathrm{c}E}\mathrm{SSB})$ | 80.6 | 0.652 | 35.67 | 0.525 |
| Ricker | none | $\alpha\mathrm{SSBe}^{-\beta\mathrm{SSB}}$ | 97.3 | 0.496 | 45.08 | 0.620 |
| | Controlling | $\alpha\mathrm{SSBe}^{-\beta\mathrm{SSB}}\mathrm{e}^{\mathrm{c}E}$ | (2) 76.5 | (2) 0.677 | 35.83 | (3) 0.508 |
| | Masking | $\alpha\mathrm{SSBe}^{-\beta\mathrm{SSB}(1+\mathrm{c}E)}$ | 78.5 | 0.664 | (2) 35.45 | 0.522 |

Figure 5.8 shows the prediction of the best fitting model (modified Cushing model with “environmental masking”) against historical data and illustrates the significantly lower recruitment associated with warmer temperatures in recent years. The model terms for spawning stock ($\log(SSB)$) and its interaction with temperature ($\log(SSB)E$) were both evaluated via an F-test to be highly

significant ($p < 0.001$). Without environmental effects (solid black curve in Figure 5.8), the model is of much poorer fit and the spawning stock biomass term is slightly positive ($\gamma = 1.24$). Such a convex relationship may imply a depensatory mechanism at low spawning stock levels, but is unlikely to be representative at higher spawning stock levels (*Iles, 1994*).

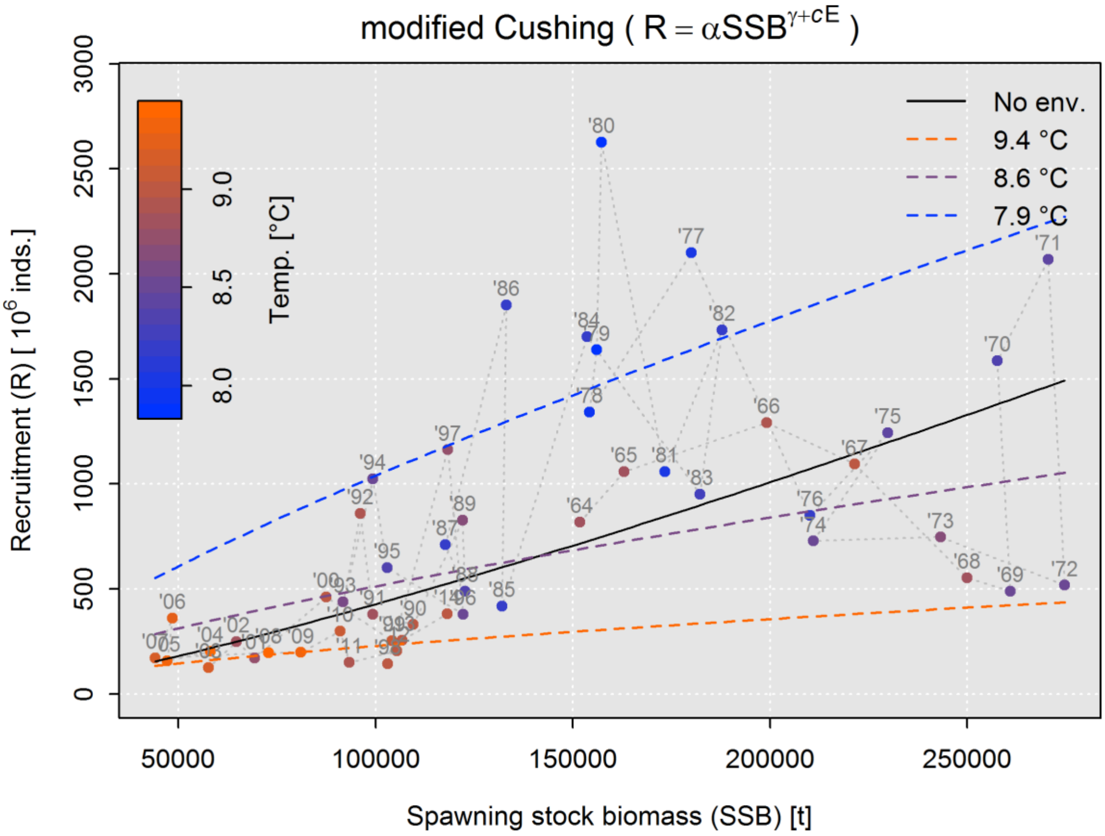

**Figure 5.8. Fitted stock-recruitment relationship for North Sea cod (modified Cushing model with "environmental masking"). Predicted recruitment for three temperatures during JFM is shown (colored dashed curves), as well as the prediction of the non-environmentally-mediated Cushing model for reference (solid black curve). Points show specific stock-recruitment observations. The colors indicate the temperature in JFM and the corresponding recruitment year is in grey text.**

Once having a model linking environmental changes to the fish stock, prognostics relating the environmental variables can be used in management. There are, however, some reasonable critiques of the incorporation of environmental covariates in predictive SRR models for management purposes. These critiques seem to prevent tactical management from including environmental drivers into stock predictions, as it was highlighted by a recent review which found that physical and biological ecosystem drivers were only implemented in the management of 24 out of more than 1200 marine fish stocks worldwide (*Skern-Mauritzen et al., 2016*). The first criticism concerns the lack of mechanistic understanding of the links between environmental factors and stock parameters and possible breaking down of correlations if circumstances change. Such breaks have been demonstrated previously for various stocks (*Myers, 1998*) and have serious consequences if environmental drivers are included into management plans (see examples in *Skern-Mauritzen et al., 2016*). However, several decades of research focusing on the mechanistic understanding of the correlative relationships have proven extremely difficult to discover precise mechanisms. Furthermore, extrapolating beyond historically observed climatic regimes is challenging independently of the detail of mechanistic understanding. As we mentioned, our approach is based on modified models incorporating different types of environmental effects related to possible mechanisms and is partially mechanistic. Moreover, we agree with *Planque et al. (2003)*, who suggested that management can still use the relationships between stock and environmental variables without fully understanding of the underlying mechanisms. The correlations found in this study are statistically robust and most of them are valid over a long time period. A regular reviewing of such correlations with newly available data would be a possible way to handle the uncertainty about the correlative relationships.

The second criticism concerns the unreliability of predictions of the environmental factors, as it was argued by *Walters and Collie (1988)* and *Planque et al. (2003)*. Reliable predictions have been mainly achieved at seasonal time scale or at the scale of several decades (e.g. *Curry and McCartney, 2001*, *Matei et al., 2012*, *Kirtman et al., 2013*). Some of the long-term predictions have been recently used in fishery related studies to predict trends over medium to long-term scales, such as decadal oscillations or climate change shifts (e.g. *Cheung et al., 2010*). However, reliable forecasts at the time scales most relevant for management, i.e. short (1-2 years) and medium (5-10 years) term, are still challenging (*Walters and Collie, 1988*). We believe that the predictability of the North Sea hydrography at short time scales can be improved in some cases, as it has been shown by *Planque et al. (2003)* . We suggest that the short-term hydrography prognostics can be achieved with statistical models, for instance, autoregressive models or linear models involving relations to climatic indices and teleconnections. One example would be the salinity of the southern and central North Sea, which was shown here to be a good environmental covariate of sprat SSB and recruitment. *Schott (1966)* and *Heyen and Dippner (1998)* showed that the salinity in the southern North Sea is correlated to river discharge with 1 year lag. Therefore, there is a potential to predict the sprat stock's dynamics with at least 1 year in advance based on the observations of river discharge. Another candidate is the temperature of the Atlantic water in the north-western North Sea, which correlates with the recruitment of the North Sea cod at 1 year lag. The inter-annual variability of the temperature in the northern North Sea may be predicted with at least one year in advance using temperature observations in the Rockall Trough in the eastern North Atlantic. Such lagged relations have been shown previously for salinity (*Becker et al., 1997*). Of course, detailed analyses are needed to estimate the explanatory power and uncertainties of such forecasts of the future trajectories of fish stocks in the North Sea.

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# 6 Modeling the effects of temperature on the survival and growth of North Sea cod (*Gadus morhua*) through the first year of life

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## 6.1 Abstract

Temperature and body size are widely agreed to be the primary factors influencing vital rates (e.g., growth, mortality) in marine fishes. We created a biophysical individual-based model which included the effects of body size and temperature on development, growth and mortality rates of eggs, larvae and juveniles of Atlantic cod (*Gadus morhua*) in the North Sea. Temperature-dependent mortality rates in our model were based on the consumption rate of predators of cod early-life stages. The model predicted 35%, 53% and 12% of the total mortality to occur during the egg, larval and juvenile stages, respectively. A comparison of modeled and observed body size suggested that the growth of survivors through their first year of life is high and close to the growth rates in ad libitum feeding laboratory experiments. Furthermore, our model indicates that experiencing warmer temperatures during early life only benefits young cod (or theoretically any organism) if a high ratio exists between the temperature coefficients for the rate of growth and the rate of mortality. During the egg stage of cod, any benefit of developing more rapidly at warmer temperatures is largely counteracted by temperature-dependent increases in predation pressure. In contrast, juvenile (age-0) cod experiences a higher cumulative mortality at warmer temperatures in the North Sea. Thus, our study adds a new aspect to the "growth–survival" hypothesis: faster growth is not always profitable for early-life stages particularly if it is caused by warmer temperatures.

## 6.2 Introduction

The very early life stages (ELSs) of marine fishes are widely appreciated as a period of high mortality. The number of survivors mainly determines recruitment success and the size of subsequent year classes in many fish stocks (*Hjort, 1914*; *Bailey and Houde, 1989*; *Houde, 2002*). The sources of mortality during the ELS are very diverse and include starvation mortality, predation mortality, unfavorable drift, developmental failure as a result of unsuitable environmental conditions, cannibalism and so forth (*Anderson, 1988*; *Leggett and Deblois, 1994*; *Houde, 2002*; *Gallego et al., 2007*; *Peck and Hufnagl, 2012*). The observed total mortality normally results from the combination of several processes and is notoriously difficult to assess because of extremely high spatial and temporal variability. Biophysical individual-based models (IBMs) have been proven to be useful tools to disentangle (and afterwards to merge again) and better understand the dominant mechanisms causing ELS mortality (*Bartsch et al., 1989*; *Werner et al., 1993*; *Miller, 2007*; *Peck and Hufnagl, 2012*; *Hufnagl et al., 2015*). Creating models that couple biological to physical processes allow us to analyze and, in the best case, quantify the role and importance of key factors controlling survival through fish ELS.

Ambient temperature and body size are among the main factors controlling vital rates of marine fishes. Temperature influences fish growth through regulating physiological rates and its effects are well studied for many species (e.g., *Fonds et al., 1992*; *Peck and Buckley, 2008*). Body size determines trophic relations (e.g., the abundances of potential prey and predators) and, therefore, influences both growth and mortality rates (*Pearre, 1986*; *Munk, 1997*). The effect of temperature on mortality rates has been so far ignored in fish ELS modeling, although it is a logical outcome of the fact that prey consumption rates of predatory fishes are temperature-dependent (*Jones, 1974*; *Andersen, 2012*). Furthermore, there is a strong evidence that the mortality rates of ELS of marine fishes depends on ambient temperature (*Pepin, 1991*; *Van der Land, 1991*; *Houde and Zastrow, 1993*). Recently, the temperature effects on zooplankton mortality have been included and tested in NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus) models (*Utne et al., 2012*; *Maar et al., 2014*). In this study, we aimed to synthesize the effect of temperature and body size on development, growth and mortality rates of fish ELS to better understand the role these factors play in offspring survival. As the case study, we chose the Atlantic cod (*Gadus morhua*) stock in the North Sea.

The cod stock in the North Sea has been at very low levels for the past 40 years and its recovery strongly depends on strong recruitment. The recruitment is “uncoupled” from the spawning stock biomass in this stock and is believed to be primarily determined by environmental (biotic and abiotic) constraints acting especially on the ELSs (*Planque and Frédou, 1999*; *Beaugrand et al., 2003*; *Olsen et al., 2011*). Various recruitment hypotheses have been championed. One-dimensional trophic models parameterized for the North Sea suggested that top-down control of cod ELSs was the principal recruitment driver (*Floeter and Temming, 2005*; *Kempf et al., 2010*; *Speirs et al., 2010*). In other studies, starvation was claimed to be the main reason of recruitment failure. Starvation mortality is often linked to the Cushing’s “match-mismatch” hypothesis (*Cushing, 1990*), but different aspects of this theory seem to be important for the North Sea cod. Based on field data, *Beaugrand et al. (2003)* concluded that the recruitment failure in the 1980s and 1990s was mainly caused by the mismatch between late larvae and juvenile of cod and the size and the abundance of their preferred prey *Calanus finmarchicus*. Based on a coupled lower-trophic level IBM, *Daewel et al. (2011)* suggested that the temporal mismatch of first feeding cod larvae and their zooplankton prey was the main reason for recruitment failure. Their modeling study predicted that the temporal match between first feeding larvae and their prey was more pronounced during cold years. This theory was supported by a negative correlation between cod recruitment and North Sea water temperatures (*Planque and Frédou, 1999*). In contrast, *Kristiansen et al. (2011)* argued that cod have a higher probability to survive through its ELS in warm years as a result of two processes. First, eggs and larvae develop more rapidly in warm years, reducing their vulnerability to predators ("bigger-is-better" hypothesis) and the cumulative mortality experienced by cohorts. Second, the temporal overlap of cod with its suitable prey was found to be longer during warm years. However, studies of *Kristiansen et al. (2011)* and *Daewel et al. (2011)* restricted their modeled period to 30 days after hatching and, thus, a considerable portion of the larval stage and all of the early juvenile stage were not represented in their models. In our modeling study, we developed a biophysical IBM of Atlantic cod which includes egg, larval and juvenile stages (up to 1 year old). We present here a new size- and temperature-dependent growth function, based on previously published laboratory experiments, and suggest an approach to incorporate temperature dependent mortality based on consumption rates of cod predators in the North Sea. We explore the interplay between growth and mortality of each developmental stage, their intra- and inter-annual variability and their influence on the length distribution of young juveniles.

## 6.3 Methods

### *6.3.1 Spawning areas, behavior and dynamic transport*

The basis of this study forms a coupled Lagrangian drift and IBM system which was coupled offline to the hydrodynamic model HAMSOM (Hamburg Shelf Ocean Model; *Backhaus, 1985*; *Pohlmann, 2006*). We used the most recent HAMSOM simulation for the North Sea with the resolution of 2.5′×1.5′ in longitudinal and meridional directions (app. 3 km × 3 km). Three-dimensional velocity fields and vertical diffusion coefficients (averaged over two M2 tidal cycles) were used to simulate the drift of particles as described by *Hufnagl et al. (2013)*, *Hufnagl et al. (2015)* except that, because of the higher spatial resolution, the present study employed a smaller horizontal diffusivity (50 $m^2$ $s^{-1}$) in the random walk parameterization.

Atlantic cod is known to spawn in the North Sea from the beginning of January until the end of April in discrete areas distributed throughout the North Sea (*CEFAS, 2001*; *Wright et al., 2003*; *Brander, 2005*; *Fox et al., 2008*). Therefore, particles simulating stage 1 cod eggs were released every 10 days between January 1st and April 30th on a regular grid (0.35˚ x 0.25˚) over the whole North Sea. In total, 92 700 particles were tracked starting at 13 release dates during the observed spawning season each year. We used a "super-individual" approach, e.g., each released particle was considered to represent an assemblage of $10^6$ equal individuals. We simulated 20 years from 1991 to 2010 with yearly simulation terminated on 30th of April of the following year, so that all released particles reached at least 1 year of age (age of recruitment of North Sea cod; *ICES, 2012*).

To properly depict the vertical distribution of cod eggs in our model, detailed information on egg buoyancy during egg development is needed. To our knowledge, such research has not been conducted for North Sea cod. Based on the studies on egg buoyancy of cod dwelling elsewhere in the North Atlantic and Baltic, we concluded that cod eggs are positively buoyant and located the upper water layer (*Kjesbu et al., 1996*; *Nisslingl et al., 1994*; *Petereit et al., 2014*). Most of the eggs are confined to the upper 20 m with strong winds or waves infrequently mixing eggs to the deeper layers (*Sundby, 1983*; *Röhrs et al., 2014*). Here we released eggs homogeneously in the upper 20 m water layer and did not allow them to sink below 20 m until they hatched (if they come deeper we set them randomly to the upper 20 m depth).

In contrast to eggs, cod larvae and juveniles are able to perform different kinds of vertical migration but this behavior is not consistently displayed (*Robb, 1981*; *Bromley et al., 1995*; *Hobson et al., 2009*). Given the complexity of this behavior and the uncertainties of the drivers as well as a proper description of spatiotemporal explicit prey field, we did not include vertical migration of larval stages in the Lagrangian drift model. *Hoeffle et al. (2013)* have shown that cod larvae are mostly confined to the upper 50 m layer, even if they perform diel vertical migration. Therefore, in our study larvae drifted passively with the water masses, including turbulent processes mimicked by a diffusive random walk, but were maintained in the upper 50 m (by means of a random replacement into a depth < 50 m as soon as the larvae were below 50 m depth). Daily temperatures experienced along drift trajectories were used to model fish growth, ontogenic development and mortality. Cod larvae kept on drifting and growing until they reached 50 mm length, the known size at which pelagic juveniles become demersal (*Bastrikin et al., 2014*). After the juvenile settlement, particles were no longer transported but continued to grow based on bottom water temperature at a settling location.

### *6.3.2 Ontogenic development and growth models*

The temperature-dependent egg stage duration of Atlantic cod was previously quantified in several studies (*Thompson and Riley, 1981*; *Geffen et al., 2006*; *Peck et al., 2009*). The equation reported by *Thompson and Riley (1981)* was used since it was obtained for the North Sea stock:

$$ESD = e^{d_1 \cdot T + d_2}, \qquad 6.1$$

Where $ESD$ is egg stage duration (days), $T$ is the water temperature (°C) and coefficients $d_1$ and $d_1$ are described in Table 6.1.

**Table 6.1 List of coefficients and their units used in this study.**

| Coefficient | Value | Unit | Corresponding equation |
|---|---|---|---|
| $d_1$ | -0.10 | $°C^{-1}$ | Eq. 6.1 |
| $d_2$ | 3.46 | no units | Eq. 6.1 |
| $\mu$ | 1 | mg | Eq. 6.2 |
| $f_1$ | 0.307 | no units | Eq. 6.3 |
| $f_2$ | 2.27 | no units | Eq. 6.3 |
| $\lambda$ | 1 | mm | Eq. 6.3 |
| $k$ | 0.06 for larvae<br>0.03 for juvenile | $day^{-1}$ | Eq. 6.5 |
| $x$ | 0.40 for larvae<br>0.25 for juvenile | no units | Eq. 6.5 |
| $a_1$ | 0.18 | no units | Eq. 6.19 |
| $a_2$ | 0.70 | no units | Eq. 6.19 |
| $b_1$ | 0.05 | $°C^{-1}$ | Eq. 6.19 |
| $b_2$ | 1.10 | no units | Eq. 6.19 |
| $c_1$ | 0.20 | $\% \ day^{-1} \cdot °C^{-2}$ | Eq. 6.19 |
| $c_2$ | 1.81 | $\% \ day^{-1} \cdot °C^{-1}$ | Eq. 6.19 |
| $c_3$ | 2.41 | $\% \ day^{-1}$ | Eq. 6.19 |

Prey dependency was not included in the model and growth of yolk-sac and exogenously feeding larvae and juveniles depended only on their size and ambient temperature. The growth model was based on the results of previously published laboratory experiments conducted at *ad libitum* feeding levels at different temperatures for cod larvae (*Otterlei et al., 1999*) and juveniles (*Björnsson and Steinarsson, 2002*; *Björnsson et al., 2007*). *Otterlei et al. (1999)* reared larvae of Norwegian coastal cod from 0.04 (yolk sac larvae) to 100 mg dry weight (approximately 3.5 to 59 mm standard length) at seven temperatures ranging from 4 to 14°C. The larvae were fed on suitable size ranges of natural zooplankton. *Björnsson and Steinarsson (2002)* and *Björnsson et al. (2007)* examined the growth of juvenile and adult Icelandic cod from 2 to $5x10^3$ g wet weight (approximately 100–1100 mm standard length) at temperatures from 2 to 19°C. Small juveniles were fed on commercial dry feed whereas larger juveniles and adults were fed on capelin (*Mallotus villosus*) and shrimp (*Pandalus borealis*).

Based on the data of *Otterlei et al. (1999)*, *Folkvord (2005)* suggested a cubic growth function for cod larvae (see Equation 1 and Figure 1 in *Folkvord (2005)*. *Björnsson et al. (2007)* proposed an exponential growth model as the best fit to their own observations and the data of *Björnsson and Steinarsson (2002)*. Both models reproduce the observations fairly well, but only within the range of weights originally examined in corresponding studies. The model of *Folkvord (2005)*, being fitted to larval growth, provides unrealistically high growth rates for juvenile and adult fishes. The model of *Björnsson et al. (2007)* for juvenile and adult growth overestimates growth rates of small larvae. Because of this incompatibility of previously suggested growth models, we merged all observations on cod growth and fitted a single growth function to them. Based on the visual inspection of the dataset, we chose a function, describing the Weibull probability density distribution (further on Weibull function):

$$SGR = c \cdot (\frac{\ln(DW_*)}{a})^{b-1} \cdot \mathrm{e}^{-\left(\frac{\ln(DW_*)}{a}\right)^b}, \qquad 6.2$$

where $SGR$ is the specific growth rate (% day$^{-1}$), and $DW_* = DW/\mu$ is a dimensionless variable, obtained by non-dimensionalizing (scaling) of the dry weight $DW$. Coefficient $\mu$ is described in Table 6.1. Such non-dimensionalizing is necessarily since a logarithmic function is involved. $a$, $b$, and $c$ are temperature-dependent parameters to be fitted.

To simulate cod length we applied length-weight conversion based on the morphometric data presented by *Peck et al.(2005)* for larval to juvenile cod between 2.5 and 124.6 mm. Here their equation was reformulated using natural logarithms:

$$ln(SL_*) = f_1 \cdot ln(DW_*) + f_2, \qquad 6.3$$

where $SL_* = SL/\lambda$ is the dimensionless representation of $SL$ (required to appropriately cancel units). Coefficients $\lambda$, $f_1$ and $f_2$ are described in Table 6.1. The weight of the newly hatched cod larvae was set to 0.04 mg (*Peck and Buckley, 2008*).

### *6.3.3 Mortality model*

Each released particle was associated with an attribute vector (AV), similar to Huse et al.( 2004):

$$\mathrm{AV} = (t, SL, DW, N_t, lat, lon, z),$$

where $t$ is the age (days post release), $lat$, $lon$ and $z$ are the latitude, longitude and depth of the super-individual, respectively. The number of individuals ($N_t$) exponentially decreases with increasing age of the super-individual:

$$N_t = N_0 \cdot e^{-M \cdot t}, \qquad 6.4$$

where $N_0$ is the initial amount of individuals (eggs) and $M$ is the instantaneous mortality rate (day$^{-1}$). We applied a combination of stage- and size-dependent mortality rates. Egg mortality was assumed to be constant $M_e = 0.20$ for all egg stages according to study of *Bunn et al. (2000)*, who re-calculated consistently observed mortality rates of cod eggs in the North Sea across several years (*Heessen and Rijnsdorp, 1989*; *Van der Land, 1991*). Weight-dependent mortality based on size-spectrum theory *Peterson and Wroblewski (1984)* was applied during larval and juvenile life-stages:

$$M = k \cdot DW_*^{-x}, \qquad 6.5$$

where $k$ and $x$ are stage-specific coefficients (Table 6.1). To model juvenile mortality we applied $k$ and $x$ from the study of *Peterson and Wroblewski (1984)*. It is generally agreed, that the larval mortality declines more rapidly with increasing size than the juvenile or adult mortality (*McGurk, 1986*, *Houde, 1997*, *Houde, 2002*). However estimates of the mortality slope are only available for few species. Here we assumed $M$ of newly hatched cod larvae (*DW*=0.04 mg) being equal to $M_e$ and $M$ of newly settled juvenile with $DW$=0.375 mg being equal to the function of *Peterson and Wroblewski (1984)* with corresponding weight. The obtained coefficients are shown in Table 6.1. We want to note that size-dependent predation, as formulated here and in studies of *Peterson and Wroblewski (1984)*, *McGurk (1986)*, *Houde (2002)*, ignores other factors affecting predation mortality (predator biomass, temperature, etc.). It can be viewed as a “mean situation”, where predator types, biomass and temperature are taken as their long-term mean.

To estimate stage-specific or cumulative mortality and survival rates for three ELSs (eggs, larvae, juvenile), we first numerically integrated instantaneous mortality over the duration of each developmental stage for each super-individual:

$$M_{cum} = \int_{t_1}^{t_2} M dt \ , \qquad 6.6$$

where $t_1$ and $t_2$ are beginning and end of a life stage, respectively. Egg stage lasts from spawn until hatch, larval stage - from hatch until settlement at 50 mm length, juvenile stage - from 50 mm to 190 mm. The length of 190 mm is the minimal length, which 1-year old cod reaches in our model. Then we calculated yearly mean cumulative mortality $M_y$ and its standard deviation $STD_y$ for the entire population and each simulated year from 1991 to 2010:

$$M_y = \frac{1}{K}\sum_{i=1}^{K} M_{cum\,i}, \qquad 6.7$$

$$STD_y = \sqrt{\frac{1}{K}\sum_{i=1}^{K}(M_{cum\,i} - M_y)^2}, \qquad 6.8$$

where $K$ is the amount of the super individuals released in a year. From the yearly mean mortalities $M_y$ we calculated long-term cumulative mortality $M_{lt}$ over 21 year of simulation and their standard deviation $STD_{lt}$. Yearly stage specific survival (in %) of the cod offspring was calculated as:

$$S = 100 \cdot \frac{\sum_{i=1}^{K}(N_{t_2})_i}{\sum_{i=1}^{K}(N_{t_1})_i} \;, \qquad 6.9$$

where $N_{t_1}$ and $N_{t_2}$ are the number of the individuals in a super individual in the beginning and end of a developmental stage correspondingly. In our model set up the amount of virtual individuals decreases due to mortality or due to drift displacement of individuals out of the model domain. To exclude the influence of drift losses, $M_y$ (Eq. 6.6) and $S$ (Eq. 6.9) were calculated only for super individuals, which settled within the model domain (51°N, 59.5°N, 4°W, 11°E).

### 6.3.4 Temperature dependent mortality

A temperature effect was incorporated into instantaneous mortality by expressing the number cod $N_{c,j}$ in a weight class *j* eaten during time period $\Delta t$ (days) through the number of predators targeting this weight class $N_{p,j}$ and their consumption rate $Cd_j$ (mg·day$^{-1}$) as:

$$N_{c,j} \cdot \overline{WW}_{c,j} = N_{p,j} \cdot fs_j \cdot Cd_j \cdot \Delta t, \qquad 6.10$$

where $\overline{WW}_{c,j}$ (mg) is mean wet weight of cod individuals in class *j*, $fs_j$ is the mean percentage of cod prey in the diet of the predator [%]. To describe the relationship between temperature $T$ (˚C) and consumption rate $Cd_j$ we assumed the commonly used exponential relation (*Jones, 1974*, *Andersen, 2012*):

$$Cd_j = Cd_{ref} \cdot e^{\delta_j \cdot (T - T_{ref})} \;, \qquad 6.11$$

where $Cd_{ref}$ is a reference consumption rate (mg·day$^{-1}$) at a reference temperature $T_{ref}$, $\delta_j$ is the temperature coefficient (°C$^{-1}$). $N_{c,j}$ in Eq. 6.10 can be expressed with the initial number of individuals $N_{0,j}$ and the mortality rate $M_j$ in the weight class *j*:

$$N_{c,j} = N_{0,j} \cdot (1 - e^{-M_j \cdot \Delta t}) \;, \qquad 6.12$$

Both $Cd_j$ and $M_j$ can be rewritten in terms of their means and anomalies. The mean mortality rate $\overline{M_j}$ was assumed to correspond to the consumption rate at mean temperature $\overline{T}$ (˚C):

$$N_{0,j}\cdot\overline{WW}_{c,j}\cdot(1-e^{-\overline{M}_j\cdot\Delta t}) = Cd_{ref,j}\cdot e^{\delta_j\cdot(\overline{T}-T_{ref})}\cdot N_{p,j}\cdot fs_j\cdot\Delta t, \qquad 6.13$$

Then the actual numbers of cod consumed can be written as:

$$N_{0,j}\cdot\overline{WW}c_{,j}\cdot(1-e^{-(\overline{M}_j+M_j^a)\cdot\Delta t}) = Cd_{ref,j}\cdot e^{\delta_j\cdot(\overline{T}+T_a-T_{ref})}\cdot N_{p,j}\cdot fs_j\cdot\Delta t, \qquad 6.14$$

where $M_j^a$ is the mortality anomaly in the weight class *j* and $T_a$ is the temperature anomaly. Solving Eqs. 6.13 and 6.14 with respect to $\mathrm{M}_\mathrm{j}^\mathrm{a}$ we obtained temperature-induced anomaly of instantaneous mortality rate:

$$M_{a,j}\cdot\Delta t = -ln(e^{\overline{M_j}\cdot\Delta t} + e^{\delta_j\cdot T_a}(1-e^{\overline{M_j}\cdot\Delta t})), \qquad 6.15$$

If we assume the temperature coefficient $\delta$ independent of predator size (an assumption which seems plausible given the lack of size-resolved measurements of $\delta$), Eq. 6.15 is valid for each weight class of cod. Therefore *j*-indices can be omitted and $\overline{M_j}$ can be replaced with size-dependent mortality from the Eq. 6.5. Temperature anomalies $T_a$ were found as differences between actual temperatures of a super individual $T$ and stage-specific long-term mean temperature $\overline{T}$ for all years and all released super individuals. Finally, size- and temperature-dependent mortality can be written as:

$$M_i = k_i\cdot DW^{-x_i}\cdot\Delta t - ln(e^{k_i\cdot DW^{-x_i}\cdot\Delta t} + e^{\delta_i\cdot(T-\overline{T}_i)}(1-e^{k_i\cdot DW^{-x_i}\cdot\Delta t})), \qquad 6.16$$

where index $i$ stands for the developmental stage (i.e. egg, larval or juvenile), $k_i$ and $x_i$ are described in Table 6.1. Temperatures $\overline{T_i}$ are shown in Table 6.2. As for the temperature parameter $\delta_i$ we proceeded in two steps. Firstly, we tested the span of all observed $\delta_i$ between 0.04 and 0.14 °C$^{-1}$ (*Jones, 1974*; *Andersen, 1999*) in a 0D model described in Section 6.4.3. Afterwards, we conducted runs with our 3D biophysical model and applied stage specific $\delta_i$ values, obtained from gastric evacuation rate studies on main predators of cod ELS in the North Sea (Table 6.2).

**Table 6.2. Main predators targeting cod early-life stages in the North Sea and the temperature-dependent coefficients of their consumption rates. Stage-specific temperature coefficients $\overline{\delta}$ averaged across all predators of each life stage were used in model simulations. The long-term mean temperature ($\overline{T}$ °C) experienced by each life stage in the North Sea is also provided.**

| Stage | Predators | δ estimates and references | $\bar{\delta}$ | $\overline{T}$ °C |
|---|---|---|---|---|
| Eggs | Herring (*Clupea harengus*)* | 0.045 - *Maes et al., 2005*<br>0.135 - *Temming, 1995* | 0.076 | 6.88 |

| | | | | |
|---|---|---|---|---|
| | sprat (*Sprattus sprattus*)* | 0.050 - *Maes et al., 2005*<br>0.080 - *Bernreuther et al., 2009* | | |
| Larvae | Herring (*Clupea harengus*)* | see above | 0.086 | 7.23 |
| | mackerel (*Scomber scombrus*)** | 0.142 - *Temming and Mergardt, 2002* | | |
| | Horse mackerel (*Trachurus trachurus*)** | 0.032 - *Temming and Herrmann, 2003* | | |
| Juveniles | Cod (*Gadus morhua*)*** | 0.110 - *Temming and Herrmann, 2003*<br>0.083 - *Andersen, 2012* | 0.090 | 9.86 |
| | Grey gurnard (*Eutrigla gurnardus*)*** | No references | | |
| | whiting (*Merlangius merlangus*)*** | 0.078 - *Andersen, 1999* | | |

**** Daan et al., 1985, Segers et al., 2007, **Van Ginderdeuren et al., 2013, *** Palsson, 1994, Greenstreet et al., 1997***

In order to quantify a relative impact of temperature on stage duration and instantaneous mortality rates, we calculated a ratio of corresponding $Q10$ coefficients for each life stage of cod:

$$R_{Q10} = \frac{Q10_{sd}}{Q10_{m}}, \qquad 6.17$$

where the $Q10_{sd}$ is the rate of change of stage duration as a consequence of increasing temperature by 10 °C and $Q10_{m}$ is the corresponding change of the instantaneous mortality rate. Temperature-dependent stage duration for cod eggs was derived directly from the Eq. 6.1, and egg mortality from Eq. 6.16. $Q10$-coefficients for durations of larval and juvenile stages were calculated numerically based on the results of our 0D model. Larval and juvenile mortality rates were obtained with Eq. 6.16 with stage specific $\delta_i$ coefficients (Table 6.2) and then averaged over corresponding size ranges.

### *6.3.5 Model validation*

Extending the model period until settlement allowed us to validate our model against the most comprehensive dataset on demersal juvenile cod, collected during the International Bottom Trawl Survey (IBTS; *ICES, 2010*). The IBTS is conducted twice a year and aims at providing information on distribution, age structure and abundances of several fish species in the North Sea. We compared observations on the length distribution of young cod in each year's 3rd quarter with modeled length distributions. Since complete 3D biophysical model results are complex and often not easy to interpret, we decided first to explore those effects using a 0D model. We started 1000 super individuals at the same day and initial weight of 0.04 mg and grew them for 180 days at constant temperatures between 2 and 18˚C. Each super individual had a batch size of $10^5$ individuals. We applied an individual parameter perturbation method to visualize how growth and mortality would influence the size spectrum of settled juveniles. Specific growth rate and mortality slope were changed by 25%, 50 % and 75%. Obtained frequencies-at-length from the model runs with perturbed parameters were compared with a baseline 0D model run, e.g. the run with ad libitum *SGR* (Eq. 6.2) and mortality slope $x$ =0.40 for larval and $x$ =0.25 for juvenile cod (Eq. 6.5). We used Bhattacharyya distance (*BD*; *Bhattacharyya, 1943*) as a measure of the similarity between observed $p$ and modeled $q$ frequencies-at-length:

$$BD = ln\left(\sum\sqrt{p \cdot q}\right). \tag{6.18}$$

Small *BD*s indicate a good and large *BD*s a poor match between observed and modeled length distributions (*Bhattacharyya, 1943*). As it is shown below in Section 6.4.3, the perturbations in growth rates appear to have a much stronger effect on the frequency-at-length of juvenile cod than the perturbations of the mortality slope. Therefore 3D-model runs were conducted with various growth rates, but same mortality slope as for the baseline run. The results of following experiments were compared with observed length distributions of young cod in each of the analyzed 20 years (1991-2010) using Bhattacharya distance (Eq. 6.18):

1) $SGR$ is equal to $ad\ libitum\ SGR$ (Eq. 6.2);

2) $SGR$ is random between zero and $ad\ libitum\ SGR$;

3) $SGR$ is random, but is higher than 25% of $ad\ libitum\ SGR$.

4) $SGR$ is random, but is higher than 50% of $ad\ libitum\ SGR$.

5) $SGR$ is random, but is higher than 75% of $ad\ libitum\ SGR$.

To obtain observed size-spectra, we extracted the catch per unit effort (CPUE) in 10 mm length classes for 0-group cod in 3rd quarter each year from ICES database (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). The maximum size of 150 mm was used to identify 0-group cod (*Kempf et al., 2013*). The proportion of the 0-group cod in the length classes was calculated based on age-length-keys (ALK, *ICES, 2013*).

According to IBTS protocol each ICES statistical rectangle (0.5˚x1.0˚ in longitudinal and meridional directions) is sampled at least twice during one survey, whereas exact position and timing of each sampling vary from survey to survey (*ICES, 2010*). To account for such sampling protocol, we sampled our model output in a similar way as the IBTS data were sampled: the date of the model sampling coincides with the date of an IBTS station; in space the modeled samples cover a square of 0.1˚×0.1˚ around each IBTS station.

The HAMSOM domain allowed us to model settled juveniles only to 59.5˚N, whereas the IBTS covers the northern North Sea up to 61.5˚N (*ICES, 2010*). To enable the comparison between our model and observations, we ignored data collected north of 59.5˚N. Since the proportion of the young cod caught north of 59.5˚N was less than 5 % of the total catch in the North Sea in all years between 1991 and 2010, this restriction does not imply any considerable information loss.

## 6.4 Results

### 6.4.1 Growth model

Parameter $a$ in Eq. 4.2 was found to be almost constant with temperature, whereas parameter $b$ increased linearly as temperature increased (Figure 6.1a). Linear and quadratic functions of temperature were found to fit parameter $c$ similarly well. We decided for the quadratic function (Figure 6.1b), because it leads to a better comparison with observed growth rates. After simple mathematical transformations the obtained growth function can be written as:

$$SGR = c \cdot (\mathrm{DW}')^{b-1} \cdot \mathrm{e}^{-(\mathrm{DW}')^{b}}, \qquad 6.19$$

where

$$DW' = a_1 \cdot ln(DW_*) + a_2,$$

$$b = b_1 \cdot T + b_2,$$

$$c = c_1 \cdot T^2 + c_2 \cdot T + c_3.$$

$\mathrm{DW}_*$ is defined in Eq. 6.2, $a$, $b$ and $c$ coefficients are given in Table 6.1.

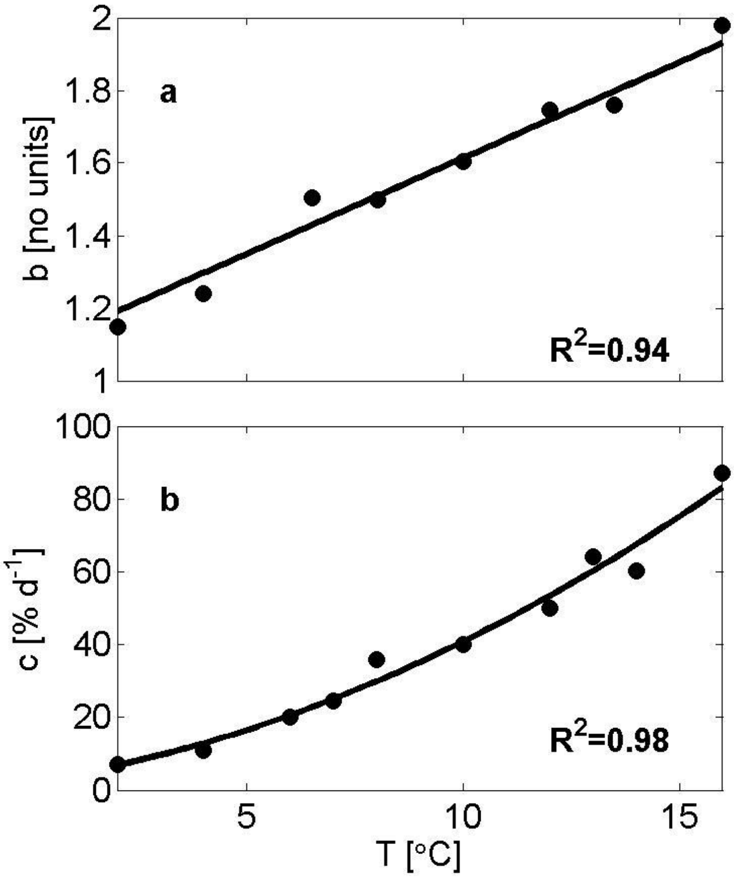

**Figure 6.1. Parameters b (panel a) and c (panel b) used to describe the specific growth rate of larval and juvenile cod (Eq. 6.2). Circles depict b and c coefficients obtained by fitting of the Weibull function to observations at different temperatures. Black solid curves are the best fit (see Eq. 6.19)**

Observed and modeled growth rates are shown exemplary for three temperatures (Figure 6.2). R-square (Table 6.3) and residuals (Figure 6.3) show that the suggested growth model accurately estimates temperature- and size-dependent growth of Atlantic cod over the observed weight range

**Table 6.3. Coefficients of determination R2 of best-fit model of *Folkvord, 2005* (second column), *Björnsson et al., 2007* (third column) and those resulted from Eq. 6.19 at different temperatures. '-' means no observations.**

| T (°C) | larvae (Folkvord, 2005) | juvenile (Björnsson et al., 2007) | Eq.6.19 (larvae/juvenile) |
|---|---|---|---|
| 2 | - | 0.91 | -/0.93 |
| 4 | 0.02 | 0.68 | 0.19/0.67 |

| | | | |
|---|---|---|---|
| 6 | 0.13 | - | 0.28/- |
| 7 | - | 0.87 | -/0.90 |
| 8 | 0.42 | 0.96 | 0.29/0.94 |
| 10. | 0.53 | 0.66 | 0.61/0.91 |
| 12 | 0.76 | 0.97 | 0.68/0.89 |
| 13 | - | 0.60 | -/0.87 |
| 14 | 0.81 | - | 0.67/- |
| 16 | - | 0.80 | -/0.86 |

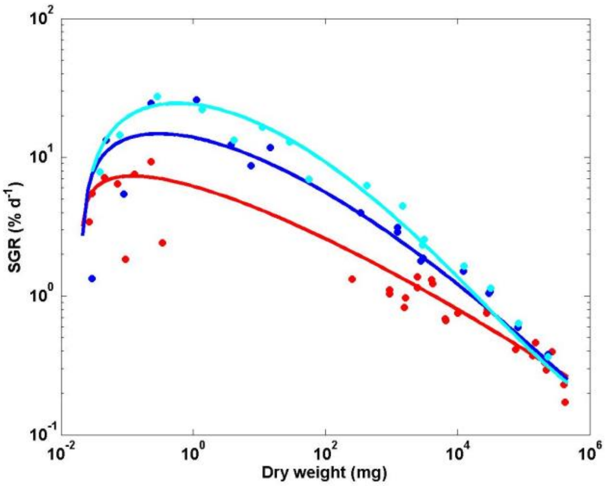

**Figure 6.2. Specific growth rate SGR (% d-1) as function of cod dry weight DW (mg) at three selected temperatures (4°C – red , 10°C – blue and 12°C – cyan), as obtained with Weibull function (Eq. 6.19). Circles are the observations from *Otterlei et al., 1999*, *Björnsson et al., 2007* at corresponding temperatures.**

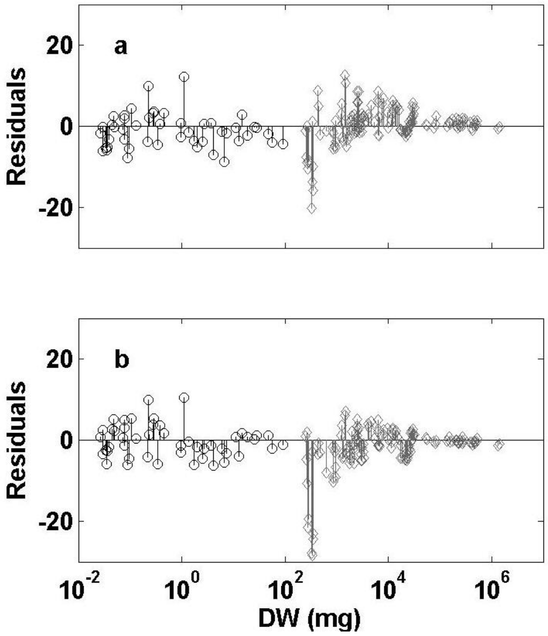

**Figure 6.3. Residuals of the estimated specific growth rates functions derived from the ad libitum growth data collected on Atlantic cod in three laboratory studies: *Otterlei et al. (1999)* (black circles), and *Björnsson and Steinarsson (2002)*, *Björnsson et al. (2007)* (grey diamonds). Panel (a) shows the residuals of fitting Weibull function (Eq. 6.19) to the combined larval and juvenile data. The residuals after fitting the growth models proposed by *Otterlei et al. (1999)* and by *Björnsson et al. (2007)* are shown on panel b. For visualization residuals with data from *Björnsson et al. (2007)* were multiplied by 10.**

### *6.4.2 Model validation: interplay between growth and mortality*

Perturbations of mortality slope (parameter *x* in Eq. 6.5) up to 75% used in our study cover almost the whole range of the observed mortality slopes (Figure 6.4), reported in *McGurk (1986)* and *Peterson and Wroblewski (1984)*. The individual parameter perturbation experiments with the 0D model indicated that ±75% perturbations in the mortality slope results in only slight changes of the frequency-at-length of young juveniles, whereas corresponding perturbations in the growth rate resulted in a considerable shift of the frequency-at-length distribution along the x-axis (Figure 6.5). The Bhattacharya distances (*BD*, Eq. 6.18) for the experiments with ±75% perturbed mortality is 0.0039, whereas the -75% perturbation of the growth rate results in a much higher BD of 3.79. Even smaller perturbations of the growth rate have a more prominent effect, than ±75% perturbations of the mortality slope (Figure 6.5). This sensitivity experiment with the 0D model clearly showed that perturbations in growth rate of comparable magnitude as perturbations in the mortality slope have a much stronger effect onto frequency-at-length distribution of modelled juveniles.

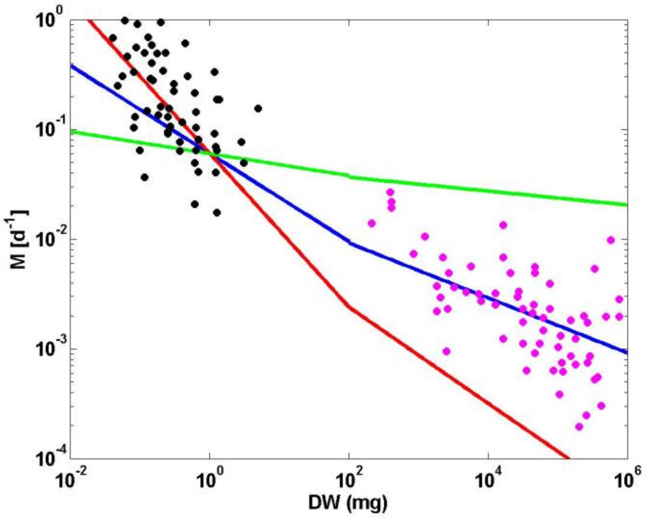

Figure 6.4. Observed (points) and modeled (lines) mortality rates M vs. fish dry weight DW. Blue lines show mortalities used in the baseline run (Eq. 6.5, x=0.40 for larvae and x=0.25 for juveniles). Red and green lines show ±75% perturbations of the mortality slope (x parameter in Eq. 6.5). Mortality rates reported for larvae and eggs (black) and juveniles and adults (magenta) were taken from literature summaries of *Peterson and Wroblewski (1984)* and *McGurk (1986)*.

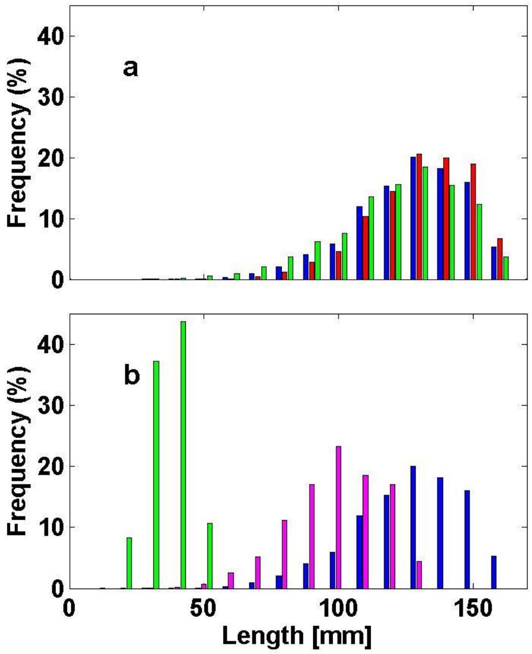

Figure 6.5. Frequencies-at-length of juvenile cod (180 days old) resulted from the 0D model experiments with perturbed mortality (panel a) and growth (panel b) rates. Blue bars on both panels depict results of a baseline model run ($ad\ libitum\ SGR$, x=0.40 for larvae and x=0.25 for juveniles). Red and green bars on panel a show frequencies-at-length obtained with -75% and +75% perturbations of x respectively. Green and magenta bars on panel b show frequencies-at-length obtained with -75% and -25% perturbations in growth rate respectively.

The 3-D model experiments applying various growth rates indicated that the best fit (lowest *BD*) to the observed frequency-at-length distributions was obtained using unrestricted (laboratory-derived) growth rates or growth rates close to them (e.g. 1995, 1996, 1997 and 2010; Figure 6.6). The runs applying random growth rates (magenta curve) and growth rates below 50% of ad libitum growth (green curve) were associated with higher *BD*s indicating lower comparability.

The *BD*s obtained with the ad libitum growth rate do not fit observed frequencies-at-length equally well (Figure 6.6, red curve). To provide more details we show here observed and modeled frequencies-at-length in 1993 (low *BD*, high fit) and 1997 (high *BD*, low fit).  Our model is able to reproduce the observations quite well, if the observed size distribution has a form similar to normal distribution (Figure 6.7a). For such length distributions, which are mostly seen in IBTS data, the *BD*s between model and observations are fairly low. The observed size-spectrum in 1997 has a skewed size distribution, which our model cannot reproduce that well (Figure 6.7b). In such years (e.g. 1992, 1997, 2001, 2007) the corresponding *BD*s are higher (Figure 6.6). However, the statement about the ad libitum growth remains valid also for those size distributions, because the *BD*s of the model run with the growth rates at or close to ad libitum growth are still lower than *BD*s of runs with other (lower) growth rates (Figure 6.6). It is beyond the scope of this paper, to find out, which combination of the growth and mortality provide the best match between modeled and observed size-spectra of small juvenile cod in each year.

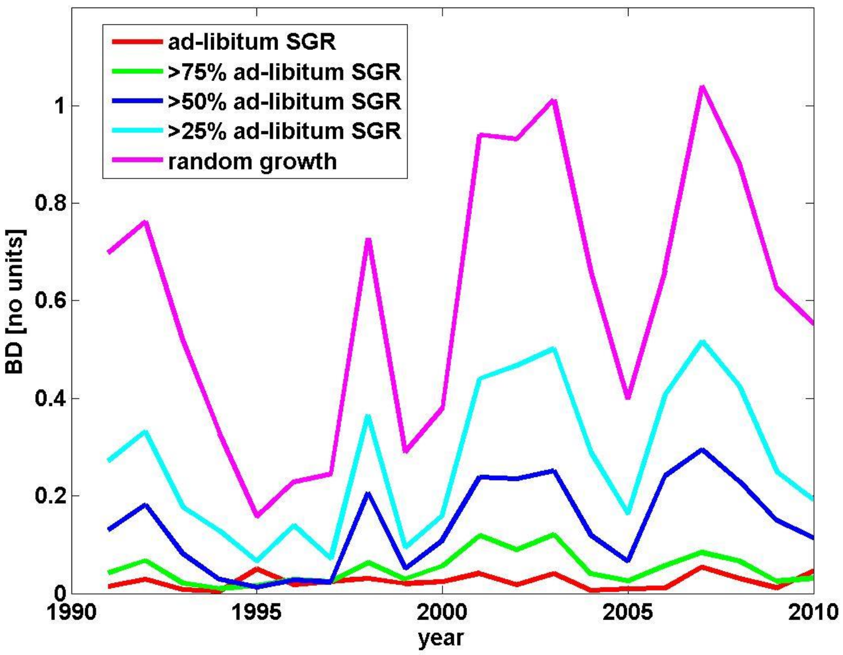

**Figure 6.6. Bhattacharyya distance (BD; Eq. 6.18) between observed and modeled frequencies-at-length of cod juveniles. Red curve shows a model run with ad libitum specific growth rates SGR (Eq. 6.19). Green curve - the run with random growth, exceeding 75% of ad libitum SGR; blue curve – run with the random SGR, exceeding 50% of ad libitum SGR; cyan curve – run with the random growth, exceeding 50% of ad libitum SGR; magenta curve – the run with random growth between 0 and ad libitum SGR.**

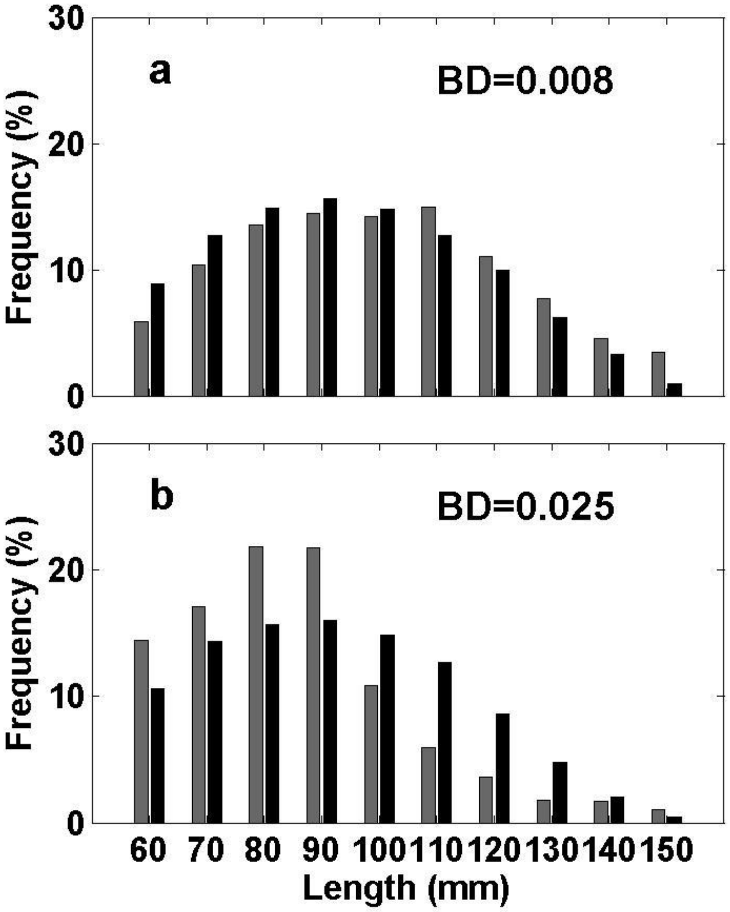

**Figure 6.7. Modeled (black bars) and observed (grey bars) frequencies-at-age of Atlantic cod juveniles in 3rd quarters of 1993 (panel a) and 1997 (panel b). Model results are obtained with ad libitum growth rates (Eq. 6.19; correspond to red curve in Figure 6.6). Corresponding Bhattacharyya Distances (BD; Eq. 6.18) are shown in each panel. Observed frequencies-at-length are obtained from IBTS data.**

### *6.4.3 Size-dependent mortality with and without temperature effect*

The durations of egg, larvae and juvenile stages are summarized in Table 6.4, where long-term mean values and their standard deviations are shown. Egg stage is the shortest one, but vulnerability of eggs to predation is very high. Modeled egg cumulative mortality is 3.4 and represents 35% of the total ELS mortality of cod in the North Sea. The larval stage duration is almost five times longer than the egg stage, but the instantaneous mortality decreases rapidly during this stage. The cumulative larval mortality is the highest one (Table 6.4) and compiles almost 53% of total ELS mortality. The survival rates of yearly offspring from hatch to settlement vary inter-annually in our model between 1 and 2.7%. The juvenile stage is the longest one, but due to very low instantaneous mortality rates during this stage the cumulative mortality is relatively low (12 % of total mortality). Our model predicts that only a very small proportion of spawned eggs (0.01 and 0.05 %) survives until recruitment age in the North Sea.

**Table 6.4. Statistics of stage-specific (cumulative) mortality rates for model runs with size-dependent mortality (SDM) and size- and temperature-dependent (STDM). For the stage durations their means and long-term standard deviations are shown. Long-term mean cumulative mortality $\overline{M}_{lt}$, standard deviation of individual mortality $\mathbf{STD_y}$ and long-term standard deviation $\mathbf{STD_{lt}}$ are shown as percentage of $\overline{\mathbf{M}}_{\mathbf{lt}}$. $\mathbf{R_{Q10}}$ is found with Eq. 6.17**

| Life stage | Stage duration | $\overline{M}_{lt}$ | $STD_y$ | | $STD_{lt}$ | | $R_{Q10}$ |
|---|---|---|---|---|---|---|---|
| | | | SDM | STDM | SDM | STDM | |
| eggs | 16±3 | 3.04 | 10.9 | 2.9 | 5.8 | 1.2 | 0.91 |
| larvae | 79±20 | 4.62 | 17.2 | 6.62 | 7.0 | 2.5 | 1.73 |
| juvenile | 215±28 | 0.95 | 12.7 | 13.2 | 1.8 | 2.1 | 0.76 |

As for variability of the stage-specific mortality, our model reveals that larval mortality not only has the largest contribution to the total mortality, but has also the strongest intra- and inter-annual variability (Table 6.4). Our results show, that all three developmental stages reveal more pronounced intra-annual (spatial and seasonal) variability, in comparison to the inter-annual one.

Including temperature effects in instantaneous mortality rates does not change stage-specific mortalities (as follows from Eqs. 6.13 and 6.14), but affects their variability (Table 6.4). To provide an insight into this effect, we illustrate the results of our 0D model with temperature coefficients $\delta$ (Eq. 6.18) between 0 (no temperature effect) and 0.14 $^{\circ}C^{-1}$ (maximal reported $\delta$). If no temperature effect is included, cumulative or stage-specific mortality decreases with increasing temperature due to reduction of the stage duration (Figure 6.8, red curves in all panels). This effect is particular prominent during larvae stage, when the growth rates are strongly temperature-dependent (Eq. 6.19 and Figure 6.1). If we apply temperature-dependent mortality with increasing δ coefficients, the slope of the red curves on Figure 6.8 is changing, showing how the effect of temperature on mortality counteracts the effect of temperature on the growth (Figure 6.8, red areas in all panels).

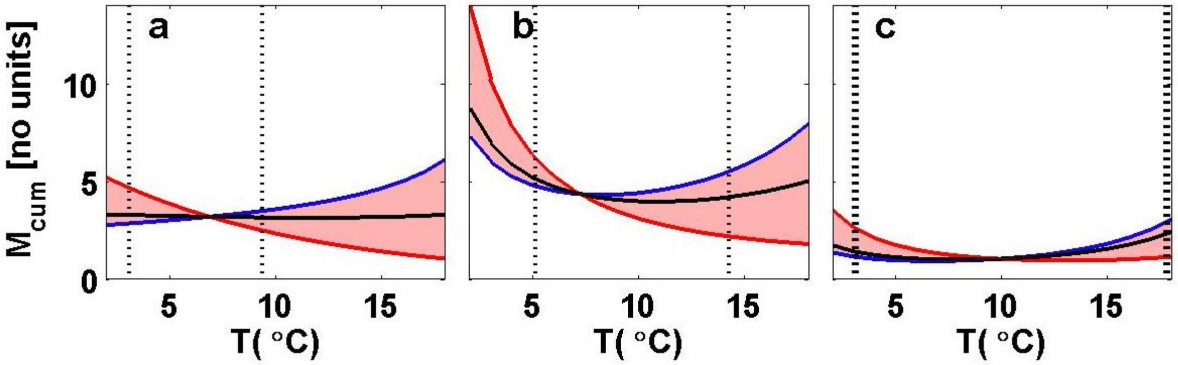

**Figure 6.8. Cumulative mortality $M_{cum}$ during egg (a), larval (b) and juvenile (c) stages as functions of temperature T (˚C). Red curves show the mortality without temperature effect being included ($\delta = 0^{\circ}\mathrm{C}^{-1}$), blue curves show temperature-dependent mortality obtained with $\delta = 0.14^{\circ}\mathrm{C}^{-1}$ . The mortality ranges, obtained with $0 \leq \delta \leq 0.14$, are shown in reddish. Black solid curves show the cumulative mortalities obtained with stage-specific δ shown in Table 2. Vertical black dashed lines show temperature ranges in the North Sea experienced by modeled individuals.**

*Q10*-ratios $R_{Q10}$ (Eq. 6.17), calculated with cod specific $\delta$ coefficients are shown in Table 6.4. $R_{Q10}$ for cod eggs is close to one, i.e. the temperature effect on mortality almost compensates the reduction in mortality due to decreasing stage duration (Figure 6.8a, black curve). This effect was also seen in the 3D model results: the intra- and inter-annual variability of egg mortality is suppressed in comparison with the case of temperature-independent mortality (Table 6.4).

$R_{Q10}$ for cod larvae in the North Sea is larger than one (Table 6.4) and therefore cod larvae, in spite of elevated instantaneous mortality, have higher survival rates in a warmer environment (Figure 6.8b, black curve). However, the decrease of the cumulative mortality with temperature is somewhat slower than in the case of temperature-independent mortality (Figure 6.8b, red curve). Similar to the egg stage, the temporal variability of larvae mortality is smaller if temperature-specific mortality is included into the 3D model (Table 6.4). In contrast, $R_{Q10}$ for juvenile cod is well below 1, e.g. cod juveniles experience higher cumulative mortality at warmer temperatures in the North Sea due to stronger predation pressure (Figure 6.8c, black curve). The intra- and inter-annual variability of juvenile mortality slightly increases with temperature, if realistic temperature effects on mortality are included into the biophysical model (Table 6.4).

To characterize the importance of different spawning dates on offspring survivorship, we calculated the relative impact of each of the 13 spawning dates on total number of survivors and averaged them over all years (Figure 6.9). If temperature-independent mortality was applied, the cumulative mortality of the individuals spawned in January-February was high due to slow development at low temperatures. Thus the impact of those spawning dates was considerably lower in comparison to the period March-April (Figure 6.9, grey bars). If instantaneous mortality was temperature-dependent, the impact of the winter months increases (Figure 6.9, black bars) due to less pronounced effects of temperature on egg and larval cumulative mortalities, whereas the impact of the spring months decreased. In other words the impact on total survivorships became more homogeneously distributed between spawning dates.

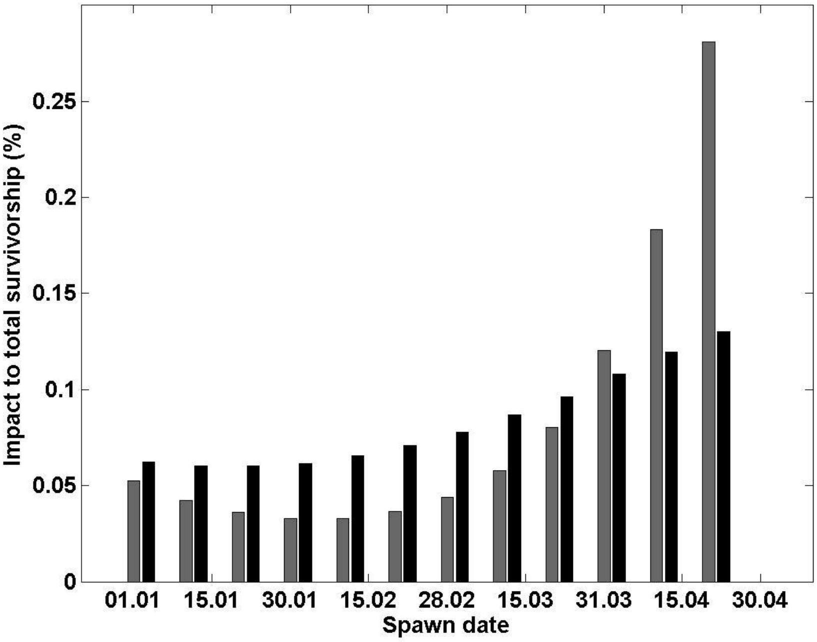

**Figure 6.9. Relative impact of eggs spawned at certain spawning date to total number of individuals surviving till recruitment. Grey bars show the results of the model run with temperature-independent instantaneous mortality; black bars – the results of the model run with temperature-dependent mortality. The impacts are averaged over the modeled period (1991-2010).**

## 6.5 Discussion

Our study is the first biophysical model to simulate complete first year of life of Atlantic cod, including pelagic eggs, larvae, and demersal juveniles. The agreement between estimated and observed growth of our model is as good as previously published models of *Folkvord (2005)* and *Björnsson et al. (2007)*, as it can be seen from descriptive statistics (R-square and residuals; Table 6.3 and Figure 6.3). In contrast to them, our growth function is applicable to the whole range of the cod sizes from 0.04 mg to 5000 g and therefore particularly suitable for modeling studies. Previous model studies on the North Sea cod (e.g. *Daewel et al., 2011*, *Kristiansen et al., 2011*) exploited more sophisticated foraging models to simulate the fish growth, but were depicted growth of cod to about 15 to 20 mm. This restriction was caused by three reasons. First, size-specific parameters of foraging models (e.g. handling time) are only well-established for small larvae (*Letcher et al., 1996*; *Huebert and Peck, 2014*). In many cases, no laboratory data exist to extend these mechanistic functions to larger body sizes. Another practical reason is that late cod larvae and juveniles display active foraging movements, requiring a different set of assumptions and equations (*Hoeffle et al., 2013*, *Fiksen and Jorgensen, 2011*). A third reason is uncertainty in the diet of large cod larvae and juveniles and difficulties of representing their suitable prey in coupled biophysical models (*Heath and Lough, 2007*, *Robert et al., 2014*). Considering these uncertainties, we decided to apply a temperature-dependent growth for the purposes of this study.

A simple temperature- and size-dependent growth function was employed to model cod growth ranging from the pelagic larvae and over the juvenile stage and through the demersal juvenile period. This allowed us to make use of the most comprehensive dataset on young cod available for the North Sea (*ICES, 2010*). The foraging success was implicitly taken into consideration by varying the modeled growth rate as a percentage of the growth determined in the laboratory for ad libitum fed cod. Our model experiments with different growth rates at ambient temperatures demonstrated that a close match between modeled and observed frequency-at-length (newly settled juveniles captured by the IBTS in the 3rd quarter from 1991 to 2010) was not possible if cod grew at rates much below those determined for ad libitum fed fish in the laboratory (Figure 6.6). This result agrees well with previous model studies and observations. *Folkvord (2005)* reported that surviving cod larvae in different regions of North Atlantic had growth rates close to the temperature-specific maximum for well-fed larvae in the laboratory. Similar results were reported for Atlantic herring larvae by *Gallego and Heath (1997)* and bluefish (*Potatomus saltatrix*) juveniles by *Hare and Cowen (1997)*: the fast-growing individuals had a higher probability to survive and, therefore, temperature-specific growth rates of individuals appeared to be fairly high. A model study conducted by *Fiksen and Jorgensen (2011)* suggested that the growth rates of cod survivors may stay high unless prey is extremely scarce, e.g. at the population scale prey availability determines the survival of larvae, but not their growth. Work on cod and haddock larvae on Georges Bank suggested that larval growth rates were prey limited during some years (*Buckley and Durbin, 2006*). A deeper insight into growth-survival relationship in cod ELS could be provided by combining drift-IBM modeling and otoliths analyses, as it has been done for other species in studies by *Hare and Cowen (1997)*, *Gallego and Heath (1997)* and *Ross et al. (2012)*.

We would like to note here, that our results do not imply that North Sea cod is never food-limited. Our model only suggests that individuals surviving through settlement appear to have growth rates similar to or slightly below ad libitum fed fish in the laboratory. The “bigger-is-better” or “growth-survival” mechanisms (*Anderson, 1988*; *Miller et al., 1988*; *Leggett and Deblois, 1994*) are likely playing a role in North Sea cod: faster development/growth reduces the time period during which eggs and larval are most vulnerable to predators and therefore increase the probability of an individual to survive. Feeding success has an important role to play here as well: poorly feeding larvae have a slower growth and are less able to escape predation and therefore have a higher probability of dying from predation. This hypothesis, however, does not exclude other sources of mortality, e.g. starvation or unfavorable drift. Therefore our findings do not contradict the results of other studies, which suggest that starvation can be an important cause of mortality of larval cod in the North Sea (*Daewel et al., 2011*, *Kristiansen et al., 2011*).

Predation (top-down) mortality has been included in biophysical models much less often than mortality caused by starvation and/or unfavorable drift (bottom-up processes, *ICES, 2009*, *Peck and Hufnagl, 2012*). This discrepancy is particularly true for previous models constructed to examine Atlantic cod in the North Sea (*Daewel et al., 2011*; *Gallego, 2011*; *Kristiansen et al., 2011*). In this study we used a combination of size and stage-dependent mortalities, which did not vary in space and time. For juvenile cod we used widely accepted size-dependent mortality rates derived from the combination of the size-spectrum theory and available observations on fish abundances (*Peterson and Wroblewski, 1984*). For cod larvae we used a steeper slope (mortality vs. size) than for juveniles, which is in agreement with observations on other fish larvae (*McGurk, 1986*, *Pepin, 1991*, *Houde, 1997*, *Houde, 2002*) and previous modeling studies (*Heath and Gallego, 1998*; *Heath et al., 2002*). Our estimates of mean total mortality of 99.96 % of cod ELS in the North Sea correspond well with the rates, suggested by *Houde (2002)*. Since our mortality model does not account for the inter-annual variability of predators and their biomass, our estimates of cumulative mortalities should be viewed as “mean” values. Furthermore, these estimates are sensitive to the choice of mean instantaneous mortality, particular for eggs and early larvae.

Validation of the modeled mortality rates is generally problematic, because of the lack of suitable observations to provide robust estimates of *in situ* mortality. Our 0D model indicated that even large perturbations in the mortality slope (up to 75 %) have only a limited influence on the frequency-at-length distribution of the modeled juvenile fish (Figure 6.5a). A similar effect was shown previously by *Cowan et al. (1996)* and *Paradis et al. (1999)*. Therefore the observed size-spectra of juvenile cod are not suitable to validate modeled mortality rates. Comparison of the modeled survival rates with the observed abundances of 0-group cod or with recruitment estimates from virtual population analyses seems us not feasible for our study. As the majority of biophysical models, we focused here only on a certain aspect of the early-life history, e.g. predation mortality and its temperature dependence. Other sources of mortality (like starvation, unfavorable drift) or sources of recruitment variability (like variability of spawning biomass or predator biomass) were ignored.

In this study we suggested a new approach to incorporate temperature-dependence into predation mortality term based on the consumption rates of potential predators (Equation 6.16). Obtained temperature-dependent mortality rates, parameterized for North Sea cod eggs and larvae, compares encouraging well with the observed mortalities, reported by *Pepin (1991)* based on broad cross-taxa data (Figure 6.10). We consider this as a strong confirmation of plausibility of our approach.

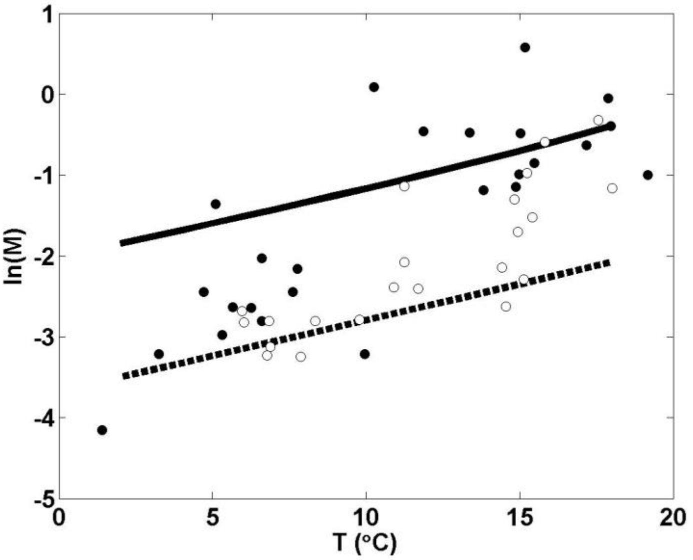

**Figure 6.10. Modeled mortality rates M for cod eggs (solid line) and cod larvae (dashed line) as compared with observed mortality rates of fish eggs (solid circles) and fish larvae (open circles) taken from *Pepin, 1991* (his Fig. 2 and 10). For comparison of larvae mortality we used DW=8.69 mg, which roughly correspond to the mean larvae size of 20 mm, used in Pepin (1991).**

Both growth and mortality rates increase with temperature. Mutual effect of these rates on stage-specific or cumulative mortality depends on the strength of the temperature dependency of both agents. Our results for North Sea cod with cod-specific temperature coefficients $\delta$ show that cod eggs do not benefit from shorter development times at higher temperatures in the North Sea, since the corresponding increase in predation mortality almost cancels the effect of reduced stage duration (Figure 6.9a, black curve). As for larvae, their cumulative mortality decreases with temperature even if temperature-specific instantaneous mortality was taken into account (Figure 6.9b). This means, that cod larvae have a higher probability to survive in warmer environment, although the reduction of cumulative mortality with temperature is weaker than in case of temperature-independent mortality. For juveniles the situation seems to be opposite: in warmer waters the increase of instantaneous mortality appears to be stronger than the increase of the growth rate and the reduction of the stage duration. Therefore cod juveniles experience a higher cumulative mortality at warmer temperatures and therefore a lower probability to survive.

North Sea cod is known to spawn over an extended period from January to April (*CEFAS, 2001*; *Wright et al., 2003*; *Brander, 2005*). Such a long spawning period allows cod to minimize the negative effect of the unpredictable timing of the zooplankton bloom, i.e. future prey availability. As *Kristiansen et al. (2011)* demonstrated, the duration of the temporal overlap between cod and it suitable prey plays an important role for the survival of the cod offspring. Therefore, hatching "too late" in spring can be less profitable because it reduces this overlap. Additionally our model indicates that the earlier-hatched larvae arrive earlier to nursery areas than their later conspecifics, although they grow more slowly. Since density-dependent mechanisms (competition for food or suitable habitat) seems to be important in nurseries of demersal fishes (*Myers and Cadigan, 1993*; *Minto et al., 2008*; *Anderson and Gregory, 2000*), earlier-spawned individuals might profit from their earlier settlement. The results of our study revealed new aspects of the reproductive strategy of Atlantic cod in the North Sea. If mortality rates are considered to be independent of temperature, spawning early in winter is not expected to be a good strategy because longer stage durations at colder temperatures will cause higher cumulative mortality. Our model predicted that the proportion of egg production in January and February yielding 1-year old juveniles is relatively low (Figure 6.9, grey bars). When mortality rates increase with increasing temperature, the proportion of early spawned progeny that survives increases considerably (Figure 6.9, black bars): cold waters provide a "refuge" compared to warm waters where predators are much more active. Therefore beyond the bet-hedging strategy of overlapping with spring plankton bloom and food competition at nurseries, the early and prolonged spawning period of cod appears favorable due to a relaxation in the strength of top-down predation pressure.

Although we considered temperature-dependent mortality in this study with respect to the North Sea cod, we can draw some general conclusions about temperature and its influence on survival of the ELS of marine fishes. Temperature influences both the rate of growth and the rate of mortality, and the interplay between these rates is critical for survival. Previous studies ignored the influence of temperature on mortality and therefore asserted that cumulative mortality decreases with temperature, because the stage duration (eggs, larvae and juvenile) becomes shorter. As we mentioned above, this hypothesis is known as "bigger is better" or "stage-duration" hypothesis (*Anderson, 1988*; *Miller et al., 1988*; *Hare, 2014*). Including temperature-dependent mortality changes this statement, because faster growing individuals in warmer environments experience higher predation mortality, which can reduce or even cancel the benefit of faster growth depending on the ratio between temperature coefficients in growth and mortality. Our results suggest that a benefit from growing in warmer environments is only given if a high $R_{Q10}$ exists.

It is important to mention here that our model study was designed to consider a certain aspect of the mortality of ELS which was previously not included within biophysical models of fish ELS (*ICES,* *2009*; *Peck and Hufnagl, 2012*). We used highly simplified assumptions about other processes which might also be temperature-dependent and play essential roles in establishing year-class mortality. For example, changes in the abundance of potential predators can strongly influence cod recruitment in the North Sea (*Speirs et al., 2010*). Another important factor is spatial and temporal overlap between cod ELS and their predators (*Kempf et al., 2010*). Changes in the abundance of predators and their overlap with ELS of cod may also be driven, to some extent, by changes in temperature. Future effort should be directed toward resolving these processes in biophysical models of the North Sea cod and other fishes, particularly in marine systems characterized by strong seasonal differences in temperature.

## 6.6 Acknowledgment

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# 7 Hot spots and refuges: The importance of adding spatiotemporal dynamics of predators within biophysical models of marine fish early life stages

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## 7.1 Abstract

Predation is one of the principle factors regulating the survival of early-life stages and recruitment success of marine fishes. The spatial dynamics of predator-prey interactions, is believed to be an important control of the magnitude of predation mortality, although it is often challenging to assess and quantify. We investigated spatiotemporal variability in predator-prey interactions by combining a biophysical model of Atlantic cod (*Gadus morhua*) early-life stages with field data on the abundance and seasonal distribution of its key planktivorous and piscivorous predators in the North Sea. Including spatially-explicit predation within simulations resulted in an increase by two orders of magnitude in the mean survival of cod early-life stages at the population level relative to simulations employing spatially homogenous predator fields. This suggests that cod early-life stages benefit from the patchy spatial distribution of its predators in the North Sea. The redistribution of predator "refuges" and "hot-spots" not only influenced the spatial pattern of cod survival through the first year of life but also the inter-annual variability in survival. Sensitivity experiments indicated that annual and seasonal changes in the distribution of predators had the strongest effect on the inter-annual variability of cod survival (25 % of its mean), followed by changes in predator biomasses (13 %) and changes in hydrographic conditions such as temperature and advection of passive life stages (9 %). These results highlight the importance of including spatial dynamics of planktivorous and piscivorous predators into models designed to understanding and predict fish recruitment and year-to-year changes in year class success. Our simulations revealed highly variable survival of cod early-life stages produced within nine known spawning areas of cod in the North Sea. These results suggest that models incorporating spatiotemporal dynamics of predation will be important in providing robust, science-based advice for spatially-explicit fishery management and marine spatial planning.

## 7.2 Introduction

Understanding recruitment success of exploited fish populations is one of the central challenges facing fisheries science and has been proved to be intractable for most stocks due to the amalgam of factors affecting recruitment (*Sissenwine, 1984*; *Sinclair, 1987*; *Fogarty et al., 1991*; *Dixon et al., 1999*; *Houde, 2008*). The condition of the parental (spawning) stock and perhaps, more importantly, processes impacting on the rates of mortality of fish early life stages (ELSs, i.e. eggs, larvae and prerecruit juveniles) are believed to be the major drivers of recruitment strength (*Bailey and Houde, 1989*; *Green, 2008*; *Mueter et al., 2007*; *Vert-pre et al., 2013*; *Szuwalski and Hollowed, 2016*). For more than a century, fisheries scientists have advanced hypotheses and our understanding of the mechanisms of fish ELS mortality (*Hjort, 1914*; *Hjort, 1926*; *Beverton and Holt, 1957*; *Houde, 2008*; *Chambers and Trippel, 1997*). Larval starvation, unfavorable drift of pelagic eggs and larvae, and predation have been postulated as major sources of mortality with predation often seen as the ultimate cause of mortality of fish early-life stages (*Hewitt et al., 1985*; *Bailey and Houde, 1989*; *Bax, 1998*; *Houde, 2002*; *Kotterba et al., 2014*).

Predation mortality of fish ELSs has been extensively studied using stomach content analyses (e.g. *Daan et al., 1985*; *Floeter and Temming, 2005*; *Segers et al., 2007*), laboratory/mesocosm experiments (e.g. *Pepin et al., 1987*; *Pepin and Shears, 1995*; *Kotterba et al., 2014*) and modelling (e.g. *Tsou and Collie, 2001*; *Huse et al., 2004*; *Speirs et al., 2010*; *Fiksen and Jorgensen, 2011*). Furthermore, analyses of the observed temporal and/or spatial co-variability of fish species are often used to conclude on their predator-prey interactions (e.g. *Huse et al., 2008*; *Hallfredsson and Pedersen, 2009*; *Minto and Worm, 2012*; *Kempf et al., 2013*) even though such “correlative” analyses have been criticized as insufficient evidence of causal relationships (*Frank and Leggett, 1985*; *Bailey and Houde, 1989*; *Rose, 2000*; *Sugihara et al., 2012*). Although previous work has greatly advanced our understanding of multiple aspects of predation (predator diets, feeding rates, predator-prey size ratios, etc.), some important aspects remain poorly examined including spatiotemporal variability of predation-prey interactions (*Ciannelli et al., 2007*; *Huse and Fiksen, 2010*; *Peck and Hufnagl, 2012*). This is due, to a large extent, to the technical challenge and high costs of simultaneously observing fish early-life stages and their predators at relevant temporal and spatial scales for quantifying the dynamics of “predator-prey overlap” (e.g. *Smith and Moser, 2003*; *Hallfredsson and Pedersen, 2009*). Mathematical modeling appears to be a promising tool to gain insight on predation process despite sparse observations and individual-based models (IBMs) have proven to be one of the most suitable modelling platforms (*Van Winkle et al., 1993*; *Heath and Gallego, 1997*; *DeAngelis and Grimm, 2014*; *Huse et al., 2008*; *Peck and Hufnagl, 2012*).

To date, 0-D (time only) IBMs have been widely applied to examine predation mortality of marine fishes ELSs (e.g. *Pepin, 1989*; *Rice et al., 1993*; *Cowan et al., 1996*; *Letcher et al., 1996*; *Fiksen and Jorgensen, 2011*). These IBMs included traits of both predators and prey and greatly advanced concepts of how larval growth rate, body size, and predator feeding mode can interact to influence the mortality experienced by larval cohorts. Since those seminal studies and the advent of biophysical 3-D IBMs for eggs and larvae of marine fish (e.g. *Werner et al., 1993*; *Heath and Gallego, 1998*, *Werner et al., 2001*), the vast majority of studies has examined mortality due to bottom-up processes such as starvation and/or unfavorable transport while predation has been much less (and often very simplistically) examined (*ICES, 2009*; *Peck and Hufnagl, 2012*; *DeAngelis and Grimm, 2014*; *Hare, 2014*). Biophysical models attempting to reproduce spatial and temporal dynamics of predators and prey and simulate their interactions have been rarely applied even within well-studied ecosystems, where data are available on the distribution, abundance and feeding rate of main predators of fish ELSs (*Huse et al., 2004*; *Wiedmann, 2010*; *Petrik et al., 2014*; *Rose et al., 2015*).

The North Sea ecosystem is one of the most well-studied shelf ecosystems worldwide, and considerable knowledge exists there on the dynamics of planktivorous and piscivorous fishes and their trophic relationships (*Greenstreet, 1996*; *Brander et al., 2016*). The Atlantic cod (*Gadus morhua*) is one of the most commercially important species in the North Sea and its stock has been depleted for several decades (*Cook et al., 1997*; *O'Brien et al., 2000*; *Horwood et al., 2006*). Since the recovery of depleted stocks strongly depends on their recruitment, recruitment dynamics of North Sea cod has been in the focus of numerous studies. Temperature-induced starvation of cod larvae (*Cushing, 1984*; *Planque and Frédou, 1999*; *Beaugrand et al., 2003*; *Nicolas et al., 2014*; *Daewel et al., 2011*) and predation (*Kempf et al., 2009*; *Kempf et al., 2010*; *Speirs et al., 2010*; *Minto and Worm, 2012*; *Hjermann et al., 2013*) have been considered to be the main processes affecting survival of cod early life stages in the North Sea. Empirical studies suggested that spatiotemporal overlap between cod ELSs and its predators might be an important factor regulating the survival of cod (*Kempf et al., 2009*; *Hjermann et al., 2013*; *Kempf et al., 2013*). But these studies used only observations on juvenile 0-group cod, and did not address mortality of eggs and larvae, stages, which are expected to be the most vulnerable to predation (*Bailey and Houde, 1989*; *Houde, 2002*). Previously published 0-D models (*Floeter et al., 2005*; *Kempf et al., 2010*; *Speirs et al., 2010*; *van Denderen and van Kooten, 2013*) and 3-D IBMs with time- and space-invariant predation (*Gallego, 2011*; *Kristiansen et al., 2011*; *Akimova et al., 2016*) did not consider how spatial dynamics of predators potentially influences mortality and survival of cod ELSs.

In the present study, we examined the importance of including spatially- and/or temporally variable predation rates on IBM-derived estimates of marine fish ELS survival using North sea cod as a case study. The wealth of data collected quarterly on the distribution and abundance of planktivorous and piscivorous predators in the North Sea offers an excellent opportunity to more thoroughly examine top-down regulation of the fish ELS survival within an IBM context. Incorporating both hydrodynamic transport and temperature-dependent growth and development of cod eggs, larvae and juveniles (*Akimova et al., 2016*), we explored the sensitivity of cod survival to abiotic (temperature and transport) and biotic (predator abundance and distribution) factors. Stage-specific survival of cod was compared across nine known spawning areas to assess their contributions to the recruitment dynamics of North Sea cod.

## 7.3 Materials and methods

Our biophysical model included three modules simulating 1) Lagrangian drift, 2) cod ELS growth and development, and 3) predation mortality. We used a super-individual approach (*Scheffer et al., 1995*) to model pelagic (eggs, larvae and young juveniles) and demersal (post-settlement, age-0 juvenile) life-stages of cod. The predation mortality was modelled combining size-dependent mortality and realistic predator consumption rates obtained from a combination of scientific survey, stock assessment and literature data. Five predators were included: Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*) preying on pelagic life stages of cod, and whiting (*Merlangius merlangus*), grey gurnard (*Eutrigla gurnardus*), and adult Atlantic cod preying on cod demersal juveniles (*Pope and Macer, 1996*; *Plirú et al., 2012*; *Daan et al., 1985*, *Kempf et al., 2013*, *Van Ginderdeuren et al., 2013*; *Speirs et al., 2010*). Our simulations were limited to the years 1991 to 1997 when survey data on the spatial distribution of predators in all four seasons were available.

### *7.3.1 Lagrangian drift and growth*

A Lagrangian stochastic drift module was coupled offline to the velocity and vertical diffusivity fields obtained from a three-dimensional circulation model of the North Sea (Hamburg Shelf Ocean Model (HAMSOM); *Backhaus, 1985*, *Pohlmann, 2006*). The coupling was similar to that described by *Hufnagl et al., 2013* except a smaller horizontal diffusivity coefficient (50 $m^2s^{-1}$) used here in the random walk parameterization to account for the finer spatial resolution of HAMSOM (3 km x 3 km). Each super-individual representing pelagic life stages of cod drifted passively but was maintained within the upper 20 m (eggs) and 50 m (larvae and pelagic juveniles) in accordance with observations of the vertical distribution of these life stages in the North Sea (*CEFAS, 2001*; *Hoeffle et al., 2013*).

Lagrangian particles were released every 10 days between 1st of January and 30th of April to cover the known spawning period of cod in the North Sea (*CEFAS, 2001*; *Wright et al., 2003*). The particles were released over the whole model domain and not merely at known spawning grounds of cod. The model domain was based on the overlap of the HAMSOM domain and the area where data were available on the distribution and abundance of cod predators (Figure 7.1). The particles represented super-individuals initialized as newly fertilized cod eggs and were released homogeneously within grid cells of 0.5° latitude and 1° longitude (ca. 56 x 56 km) and at random depths between 0 to 20 m. These grid cells correspond to the statistical rectangles used in the surveys conducted by the International Council of the Exploration the Sea (ICES; *ICES, 2010*). Within these spatial units (known as “ICES rectangles”), the consumption rate of predators was calculated and obtained individual survival estimates were aggregated (see chapter 7.3.2). We released 6500 super-individuals in each ICES rectangle on each of 13 spawning dates (e.g. 13,351,000 super-individuals per year) in each of 7 years. The integration for each modelled year was stopped when all super-individuals reached the age of one year, the age of cod recruitment in the North Sea (*ICES, 2012*).

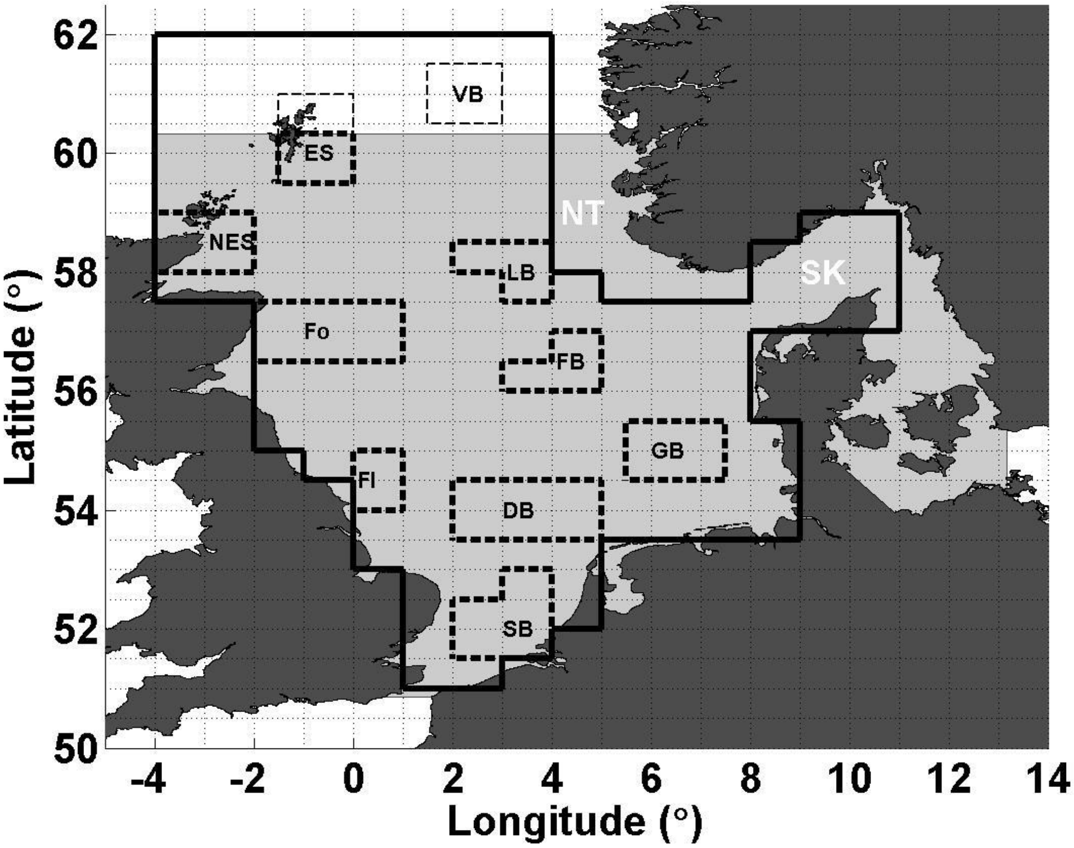


**Figure 7.1. The map of the North Sea including 1) the domain of the hydrodynamic model (HAMSOM) (light grey) and 2) region where survey data on predators was available (solid black line - North Sea International Bottom Trawl Survey (NS-IBTS). The domain of the biophysical model was the overlap between regions 1 and 2. Dotted lines indicate ICES statistical rectangles. Dashed lines show known spawning grounds of North Sea cod: ES - East of Shetland, NES - northeast of Scotland, Fo – Forties, Fl- Flamborough, DB - Dogger Bank, SB - Southern Bight, GB - German Bight, FB - Fisher Bank and LB - Ling Bank (see Table 7.3). Spawning grounds outside of the model domain, Viking Bank (VB) and the northern part of the ES are shown with thin dotted lines. SK (Skagerrak), NT (Norwegian Trench) depict the areas mentioned in text.**

Temperatures experienced by super-individuals along their drift pathways were used to model individual growth and development of cod ELSs. The model included temperature-dependent egg stage duration (*Thompson and Riley, 1981*) and growth of larvae and juveniles following the approach of *Akimova et al. (2016)*: daily growth rate of cod larvae and juveniles randomly varied between 75%

and 100% of the temperature-dependent "ad-libitum" specific growth rate ($SGR$, d$^{-1}$) reported by *Akimova et al. (2016)*:

$$DW_{t2} = DW_{t1} + rand[0.75, 1] \ \cdot SGR \cdot DW_{t1} \cdot \Delta t \ , \tag{7.1}$$

where $DW_{t1}$ and $DW_{t2}$ are the dry weights of a modelled individual at two successive time steps $t1$ and $t2$, $rand[0.75, 1]$ is a random number between 0.75 and 1 and $\Delta t$ is the time step (1 day). *Akimova et al. (2016)* demonstrated that the best match between observed and modelled size distributions of cod juveniles was obtained when modelled growth rates were close to those achieved by fish fed *„ad-libitum"* during laboratory rearing (*Otterlei et al., 1999*, *Björnsson and Steinarsson, 2002*, *Björnsson et al., 2007*).

The dry weight (Eq.7.1) was converted to the body length using Eq. 3 in *Akimova et al. (2016)*. When simulated larvae reached the length of 20 mm, they became pelagic juveniles. At 50 mm length, pelagic juveniles ceased to drift, settled to the bottom and became demersal juvenile growing at rates dictated by the bottom water temperature at their settlement site.

### 7.3.2 Predation mortality

Each released super-individual represented a set of $N_0$ identical cod individuals. The number of individuals within a super-individual decreased with the time due to predation mortality $M$ (d$^{-1}$):

$$N_{t2} = N_{t1} e^{-M\Delta t}, \tag{7.2}$$

where $N_{t1}$ and $N_{t2}$ are the numbers of the individuals in a super-individual at time steps t1 and t2. Instantaneous mortality M was parameterized based on theoretical considerations of size-dependent mortality (*Pauly, 1980*; *Peterson and Wroblewski, 1984*; *Lorenzen, 1996*) and realistic estimates of the consumption rate of predators. Size-dependent mortality rate $\overline{M}$ (d$^{-1}$) was parameterized following *Peterson and Wroblewski (1984)*:

$$\overline{M} = k \cdot DW_*^{-x}, \tag{7.3}$$

where $DW_*$ is a dimensionless variable, which corresponds to the dry weight DW in mg (non-dimensional since an exponential function of DW is involved). Coefficients $k$ and $x$ were taken from the previous studies on predation mortality of cod and other fish ELSs (Table 7.1). As mentioned by *Akimova et al. (2016)*, the coefficients $k$ and $x$ were obtained by combining available observations and therefore are not linked to any particular predator biomass or environmental condition in the North Sea. They can be viewed as estimates of the long-term, mean mortality.

**Table 7.1 Parameterization of the size-dependent instantaneous mortality (Eq. 7.3) of cod eggs, larvae and juveniles.**

| Early-life stage | k | X | Reference |
|---|---|---|---|
| Egg | 0.20* | 0 | *Bunn et al. (2000), ICES (1994)* |
| Larval | 0.06 | 0.40 | *Akimova et al. (2016)* |
| Juvenile | 0.03 ** | 0.25** | *Peterson and Wroblewski (1984)* |

*** - values were taken as averages from the studies, cited in the reviews of *Bunn et al. (2000)* and *ICES (1994)***

**** - adapted from Peterson and Wroblewski (1984) for the units, used in this study**

To incorporate the observed biomass and spatial distribution of the main predators into the model, we first calculated the daily consumption of each predator *i* in each year *j* using an approach similar to *Mackinson and Daskalov (2007)*:

$$C_{ij} = C_{ind\,i} \cdot \alpha_i \cdot \mathrm{B}_{ij} \cdot l_{ij}, \qquad 7.4$$

where $C_{ind\,i}$ ($d^{-1}$) is the individual daily consumption rate of predator $i$ as a proportion of its body weight per day, $\alpha_i$ is the percentage of cod ELSs in the diet of predator *i*, $\mathrm{B}_{ij}$ (mg) is its total stock biomass and $l_{ij}$ is the proportion of the biomass within the predator length range targeting cod ELS. The parameter $C_{ind\,i}$ was temperature-dependent in agreement with the previous laboratory and field studies (e.g. *Andersen, 1999*, *Temming and Herrmann, 2003*):

$$C_{ind\,i} = C_{ref\,i} \cdot e^{\delta_i \cdot (T - T_{ref})}, \qquad 7.5$$

where $C_{ref\,i}$ ($d^{-1}$) is a reference consumption rate at temperature $T_{ref}$ (°C) and $\delta_i$ is predator-specific temperature coefficient (°$C^{-1}$). The mean temperature in the North Sea was taken as $T_{ref}$ (°C), following *Maar et al. (2014)*. Estimates for $C_{ref}$, $\delta$ (Eq.7.5) and $\alpha$ (Eq.7.4) for each predator were compiled from the literature (Table 7.2). Since cod ELSs constitute only a small part of the diet of all predators considered in this study (see $\alpha$ in Table 7.2), no functional response of predators was taken into account and consumption rates $C_{ind\,i}$ were assumed to be density-independent.

**Table 7.2. Reference daily consumption rate $\mathbf{C_{ref}}$ (d$^{-1}$), temperature coefficient $\boldsymbol{\delta}$ ($^\circ\mathbf{C}^{-1}$), the percentage $\boldsymbol{\alpha}$ ( %) of cod ELSs in the diet and length range (mm) of all predators preying on cod ELSs and included in this study. References are listed below.**

| Predator | ELS | $C_{ref}$ | $\delta^{(1)}$ | $\alpha^{(3)}$ | length range |
|---|---|---|---|---|---|
| herring | Eggs, larvae and pelagic juveniles | 1.24 | 0.09 | 4.00 | all lengths |
| sprat | Egg | 1.24 | 0.07 | 4.00 | all lengths |
| grey gurnard | demersal juveniles | 1.49 | 0.09$^{(2)}$ | 2.80 | 150-350 |
| whiting | demersal juveniles | 1.48 | 0.08 | 0.51 | 120-500 |
| cod | demersal juveniles | 1.44 | 0.10 | 4.06 | 300 -1200 |

**(1) values were taken as averages from the studies, compiled by *Akimova et al. (2016)***

**(2) no estimates of δ were available for grey gurnard, the value is taken as average for other gadoid predators: cod and whiting**

**(3) based on the studies of *Greenstreet (1996)* and *de Gee and Kikkert (1993)***

The total stock biomasses $B_{ij}$ were obtained from the recent North Sea stock assessments (*ICES, 2015*; *ICES, 2015*) except for grey gurnard, a species not assessed prior to 2016, where the output from the North Sea Stochastic Multi-Species Model (SMS, *Kempf et al., 2010*) was used. The length range $l_{ij}$ (Eq. 7.4) of each predator targeting cod ELSs was obtained as follows. Herring and sprat are planktivorous fish species and all body lengths of adults were assumed to feed on pelagic life stages of cod (*Pommeranz, 1979*; *Daan et al., 1985*; *Hopkins, 1988*). The size range of each predator preying on demersal juvenile cod was obtained from previously reported prey/predator length ratios (*Floeter and Temming, 2005*; *de Gee and Kikkert, 1993*) and the average size of juvenile cod at settlement (50 mm, *Bastrikin et al., 2014*) and at the end of the first year of life in the North Sea (200 mm, *Rindorf, 2002*). Using these length ranges, the proportion $l_{ij}$ of the total stock biomass was calculated based on the length measurements obtained from the North Sea International Bottom Trawl Survey (NS-IBTS, *ICES, 2010*).

The NS-IBTS is a groundfish survey that provides information needed to assess the status of the commercial fish stocks in the North Sea (*ICES, 2010*). Groundfish samples were collected at random locations within ICES statistical rectangles, covering almost the entire North Sea excluding the deep Norwegian Trench in the east (Figure 7.1). The ICES database for trawl surveys (*DATRAS, 2017*) includes catch per unit of effort (CPUE) per species, length class and haul. The NS-IBTS has been carried out during the 1st quarter of the year between 1965 and 1990, quarterly from 1991 to 1997, and twice a year (1st and 3rd quarters) from 1998 to the present. We used the period from 1991 to 1997, when quarterly data were available. Missing data were interpolated as described in Appendix A.

In the model simulation with homogeneous predator distribution, we used the constant proportion of the total biomass of each predator $i$ within each ICES rectangle *n* and quarter *k* as:

$$X_{ijkn} = \frac{1}{R}, \tag{7.6}$$

where R is the total number of sampled ICES rectangles (R=158). In the simulations with the spatially-explicit realistic predation, we used the observed spatial distribution of the CPUEs within relevant length ranges of each predator. Haul-based CPUEs were summed up within ICES rectangles and quarters and the proportion of total CPUE in each ICES rectangle was calculated as:

$$X_{ijkn} = \frac{\mathrm{CPUE}_{l\,ijkn}}{\sum_n CPUE_{l\,ijkn}}. \tag{7.7}$$

The proportion $X_{ijkn}$ was used to model predation consumption rate of each predator within ICES rectangle *n*:

$$C_{ijkn} = C_{ij} \cdot X_{ijkn}. \tag{7.8}$$

The quarterly values of predator consumptions $C_{ijkn}$ were assumed to occur at the midpoint of each quarter (15th of February, May, August and October) and were linearly interpolated between these dates to obtain daily consumption rates.

The predator-specific daily consumption rates $C_{ijkn}$ (Eq. 7.8) were used to calculate daily consumption rate of cod eggs $C_{eg}$ (consumed by herring and sprat), larvae $C_{la}$ and pelagic juveniles $C_{pel\,ju}$ (consumed by herring), and demersal juveniles $C_{dem\,ju}$ (consumed by adult cod, whiting and grey gurnard). These consumption rates were converted to corresponding instantaneous mortality rates ($M_{eg,}$ $M_{lar}$, $M_{pel\,ju}$, $M_{dem\,ju}$) using an approach similar to *Akimova et al. (2016)*. We omitted here the subscripts corresponding to the developmental stages, because the conversion is identical for all stages. Instantaneous mortality $M$ is related to the consumption rate $C$ as:

$$N_0 \cdot WW \cdot (1 - e^{-M\Delta t}) = C \cdot \Delta t, \tag{7.9}$$

where $N_0$ is the initial number and $WW$ is the mean wet weight of cod individuals. Eq. 7.9 can be written in term of the long-term mean mortality $\bar{M}$ and mean consumption rate $\bar{C}$:

$$N_0 \cdot WW \cdot (1 - e^{-\bar{M}\Delta t}) = \bar{C} \cdot \Delta t, \tag{7.10}$$

where $\bar{C}$ is consumption averaged across the entire simulation period. Solving Eqs. 7.9 and 7.10 with respect to $M$ we obtained:

$$M = -\frac{1}{\Delta t} \cdot \ln(1 + \frac{C}{\bar{C}} \cdot (e^{-\bar{M}\Delta t} - 1)), \qquad 7.11$$

where long-term mortality rate $\bar{M}$ can be substituted as a function of the cod size (Eq. 7.3 ):

$$M = -\frac{1}{\Delta t} \cdot \ln(1 + \frac{C}{\bar{C}} \cdot (e^{-k \cdot DW_{*}{}^{-x}\Delta t} - 1)). \qquad 7.12$$

Constraints of the logarithmic term in Eq. 7.12 are discussed in Appendix C. To estimate cumulative mortality $M_{cum}$ and survival $S$ during particular developmental stage we integrated instantaneous mortality $M$ (Eq. 7.12) over the stage duration D of a super-individual:

$$M_{cum} = \sum_{D} M\Delta t, \qquad 7.13$$

$$S = e^{-M_{cum}}. \qquad 7.14$$

By substituting stage-specific predator consumption, parameters *k* and *x* (Table 7.2) and super-individual specific stage durations D in Eqs. 7.12-7.14, we obtained survivals during the egg ($S_{eg}$), larval ($S_{lar}$), and pelagic and demersal juvenile ($S_{pel\ ju}$and $S_{dem\ ju}$) stages. Survival $S_r$ of a super-individual *r* over the entire early-life period was found by multiplying the survival during four developmental stages:

$$S_r = S_{eg} \cdot S_{lar} \cdot S_{pel\ ju} \cdot S_{dem\ ju}. \qquad 7.15$$

### *7.3.3 Sensitivity experiments*

Sensitivity experiments were conducted to estimate the relative importance of biotic and abiotic factors on inter-annual variability of cod ELS survival in the North Sea. Three factors were tested:

Run 1 “Hydrography” used fixed predator biomasses and spatial distributions but variable hydrographic conditions from HAMSOM,

Run 2 “Predator Biomass” used fixed hydrographic conditions and fixed predator distributions $X_{ijkn}$ (Eq. 7.7) but the biomass of predators $\mathrm{B}_{ij}$ (Eq. 7.4) changed annually, and

Run 3 “Predator Distribution” used fixed hydrographic conditions and fixed predator biomasses $\mathrm{B}_{ij}$but the distribution of predators $X_{ijkn}$ varied accordingly to observations.

Fixed values of the total biomass $\mathrm{B}_{ij}$ and quarterly distribution of predators $X_{ijkn}$were equal to the mean values for the period 1991-1997. Fixed hydrographic conditions were based on HAMSOM output for 1992. In that year, the North Atlantic Oscillation Index (NAOI) was close to its long-term mean and, given the strong correlation between the NAOI and North Sea hydrography (*Becker and Pauly, 1996*, *Hjøllo et al., 2009*), hydrographic conditions were considered to be “average” in this year.

### *7.3.4 Analyses of the model results*

To examine the spatial variability of the survival individual survival estimates $S_r$ (Eq. 7.15) were averaged within cohorts and within ICES rectangles, where the super-individuals were released. Obtained estimates of the mean survival $S_n$ were compared between the homogeneous and realistic simulations. Due to the prevailing cyclonic water circulation of the North Sea, a substantial number of super-individuals released in the northern and eastern areas drifted out of the model domain (*Otto et al., 1990*). For those super-individuals, it was not possible to estimate individual survival $S_r$. To ensure statistical stability of the survival estimates $S_n$, ICES rectangles were only included in analyses if the number of super-individuals within a cohort started there remained above 1500 (i.e., 25% of initial super-individuals) by the end of a modelled year (see Appendix B).

To examine the temporal variability of the modelled survival we calculated cohort-specific survival $S_c$ in five scenario simulations (homogeneous and realistic predation distribution and 3 sensitivity simulations) by averaging $S_n$ obtained for each released date over all ICES rectangles. Yearly mean ELS survival $S_y$ was found by averaging $S_c$ over all 13 cohorts within a year. Following statistics of $S_y$ were calculated: the mean survival over the entire simulated period ($\overline{S_y}$), the coefficient of variation of the yearly-mean survival ($c_v$), standard deviations of the yearly mean survival ($\delta_y$), of cohort-specific survivals for each year ($\delta_c$) and of cohort-specific survival over the simulated period ($\bar{\delta}_c$). For the sensitivity experiments these statistics were calculated for each of four developmental stages separately, using stage-specific survival estimates $\mathrm{S}_{eg}$, $S_{lar}$, $S_{pel\ ju}$ and $S_{dem\ ju}$ (Eq. 7.15).

To reveal the driving mechanisms behind the inter-annual differences in survivals $S_y$ in the simulations with the homogeneous and realistic predator distributions we calculated Pearson correlation coefficients between $S_y$ and: i) cumulative predator biomass, ii) stage-specific predator biomass, and iii) mean temperature over the whole year at all depths, and iv) mean temperature experienced by pelagic life stages, taken as the mean temperature from January to June in the upper

20 m, which roughly correspond to the duration and depth of pelagic life-stages of cod. Additionally we estimated the total time (in days) super-individuals spent under various predation conditions in the realistic simulation. We divided all grid cells into two groups:

Group A: cells where predation consumption was higher than in the homogeneous simulation ($X_{ijkn} \geq \frac{1}{R}$)

Group B: cells where predation consumption was lower than in the homogeneous simulation ($X_{ijkn} < \frac{1}{R}$).

We tallied the amount of days each super-individual spent in both categories of cells ($t_r(group\ A)$ and $t_r(group\ B)$), summed them over all released super-individuals and calculated the ratio Q:

$$Q = \frac{\sum t_r(group\ A)}{\sum t_r(group\ B)} \qquad 7.16$$

To examine the ELS survival at cod spawning grounds, $S_r$ obtained in the simulation with the realistic predation were averaged within cohorts and known spawning grounds in the North Sea (Figure 7.1, Table 7.3). Nine of the reported spawning grounds (*Daan, 1978*; *Brander, 1994*; *Fox et al., 2008*; *CEFAS, 2001*; *Wright et al., 2003*; *González-Irusta and Wright, 2016*) were analyzed (those which had been reported in two or more studies and where at least half of the spatial extent occurred within the model domain). Obtained cohort-specific survival $S_{sa}$ within each spawning area were pooled by year as well as by release time across years. Yearly mean survival within spawning areas $S_{sa\,y}$ were calculated as well as the mean survival over the entire simulation period $\overline{S_{sa}}$. We analyzed the seasonal pattern of the cohort-specific survival in order to identify periods of predominantly low or high survival. Moreover, retention index $RI_{sa}$ associated with the spawning areas was assessed as a mean percentage of cohorts released within the area and for which at least 1500 super-individual (i.e., more than 25% of initially started super-individuals) remained in the domain by the end of a modelled year.

**Table 7.3. Spawning areas of North Sea cod used in this study. The names of the spawning areas were taken from the cited literature. The location of the areas is shown in Figure 7.1.**

| Spawning ground | Abbreviation | References |
|---|---|---|
| East of Shetland | ES* | 4, 7 |
| Northeast of Scotland | NES | 2, 7 |
| Forties | Fo | 2,3,7 |
| Flamborough | Fl | 1, 7 |
| Dogger Bank | DB | 1, 2, 3, 4, 6 |
| Southern Bight | SB | 1, 2, 3, 6 |
| German Bight | GB | 1, 3 |
| Fisher Bank | FB | 2, 4, 7 |
| Ling Bank | LB | 2, 4, 7 |
| Viking Bank | VB** | 2, 5 |

**1 = *Brander (1994)*, 2 = *CEFAS (2001)*, 3 = *Daan (1978)*, 4 = *Fox et al. (2008)*, 5 = *González-Irusta and Wright (2016)*, 6 = *Lelièvre et al. (2014)*, 7 = *Wright et al. (2003)*. *Only southern half included, ** not included.**

## 7.4 Results

### *7.4.1 Cod survival and homogeneous versus realistic predator distributions*

Our simulations with the homogeneous and realistic predator distributions resulted in substantially different estimates of survival of cod early-life stages (Figure 7.2). Mean survival in the realistic simulation ($\overline{S_y}$ =6.65%) was two orders of magnitude higher than that in the homogenous simulation ($\overline{S_y}$ =0.017%). The standard deviations calculated among the years ($\sigma_y$) as well as within seasons ($\bar{\sigma}_c$) were larger in the realistic simulation compared to the homogenous one (Figure 7.2). Mean annual survival $S_y$ obtained in the homogeneous simulation was highly correlated to the biomass of predators on the pelagic life-stages of cod (eggs, larvae and young juveniles), whereas no significant relationship was observed between ELS survival and the biomass of predators on cod demersal juveniles (Table 7.4). There was no relationship between mean annual survival and predator biomasses when the realistic predator distributions were used. In both scenarios, ELS survival was not significantly related to the annual mean water temperature (Table 7.4). The ratio Q (Eq. 7.16) obtained in the realistic simulation varied between 1.6 and 4.5 during the simulated period (Figure 7.3).

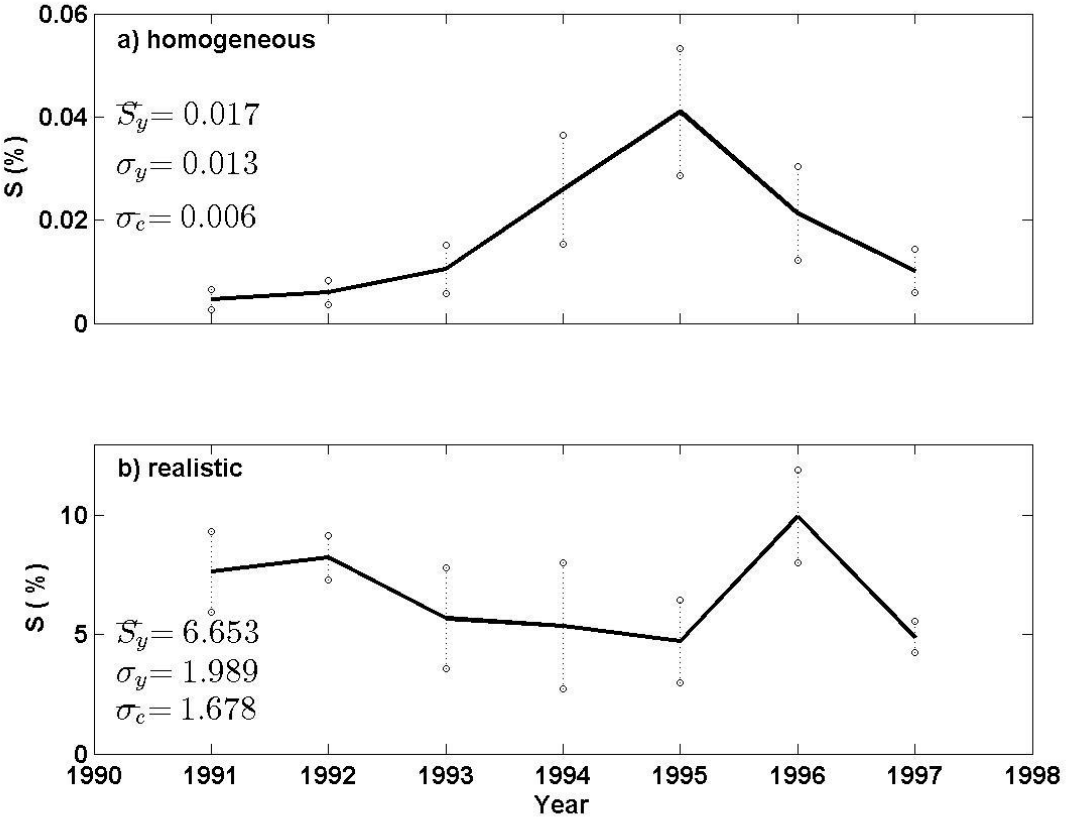


**Figure 7.2. Time-series of yearly mean ELS survival $S_y$ (%) for the homogeneous (a) and realistic (b) simulations. Dashed lines show the standard deviation $\delta_c$ of the cohort-specific survival in each year. Mean survival over the whole simulated period ($\overline{S_y}$), standard deviations of the yearly mean survivals ($\delta_y$) and the mean cohort-specific deviation ($\overline{\delta_c}$) are shown.**

**Table 7.4. Coefficients of correlation and corresponding p-values found between annual mean ELS survival $S_y$ in the homogeneous and realistic simulations from one side and five explanatory variables: 1) total predator biomass, 2) biomass of pelagic predators, 3) biomass of demersal predators, 4) yearly mean temperature over all depths (T1), and 5) mean temperature experienced by pelagic life stages, taken as the average from January to June in the upper 20 m (T2). Significant correlations (p<0.05) are highlighted.**

| Explanatory Variable | Homogeneous predation | Realistic predation |
|---|---|---|
| total predator biomass | **-0.93 (p=0.003)** | 0.25 (p=0.59) |
| biomass of pelagic predators | **-0.92 (p=0.003)** | 0.37 (p=0.41) |
| biomass of demersal predators | 0.70 (p=0.079) | -0.50 (p=0.24) |
| T1 | -0.35 (p=0.440) | -0.26 (p=0.57) |
| T2 | -0.33 (p=0.478) | -0.33 (p=0.48) |

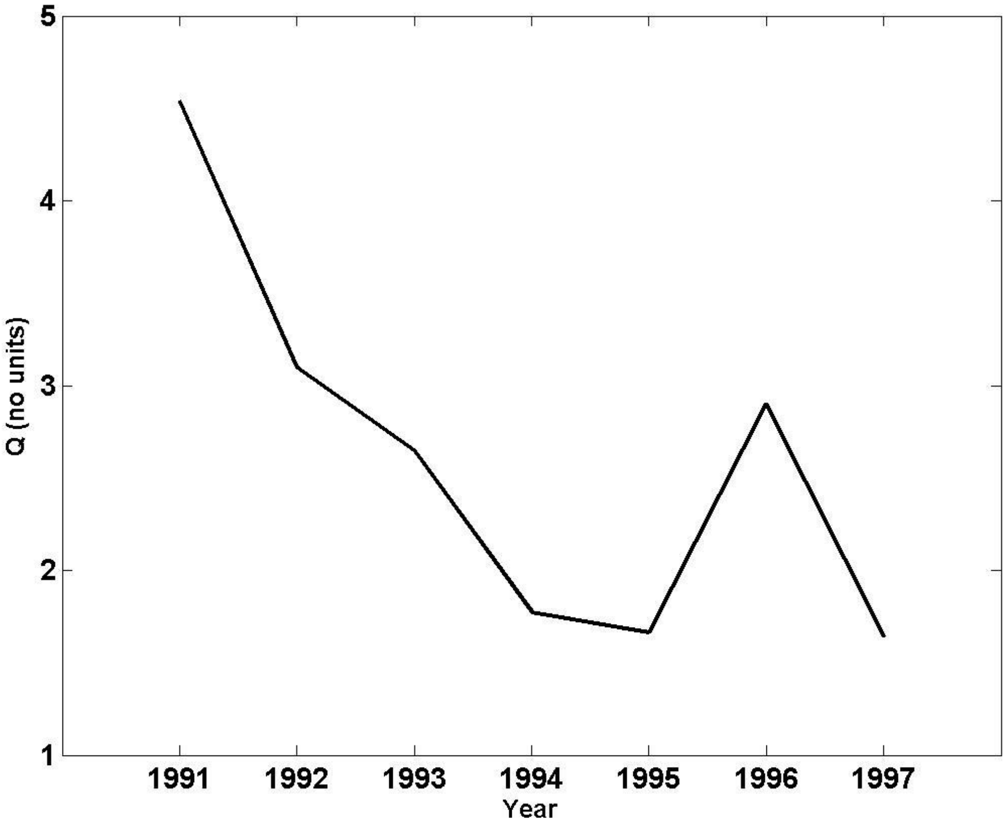


**Figure 7.3. Q-ratio (Eq. 7.16) obtained in the simulation with the realistic predation distribution.**

The spatial distribution of survival $S_n$ differed substantially between the homogenous and realistic scenario simulations (Figure 7.4). Even when viewed in relation to the known spawning areas, no consistent pattern emerged. To illustrate substantial spatial and scenario differences in survival, two contrasting examples are provided for super-individuals released at two grid cells (Figure 7.5, black rectangles) on 20th February 1992. In the homogeneous simulation, super-individuals released in the northern grid cell (Figure 7.5a, grid cell 1) had a higher mean survival than those released in the southern grid cell (Figure 7.5a, grid cell 2). The opposite was predicted in the simulation with the realistic predator distributions: the $S_n$ in grid cell 1 was lower than that in the grid cell 2 (Figure 7.5b).

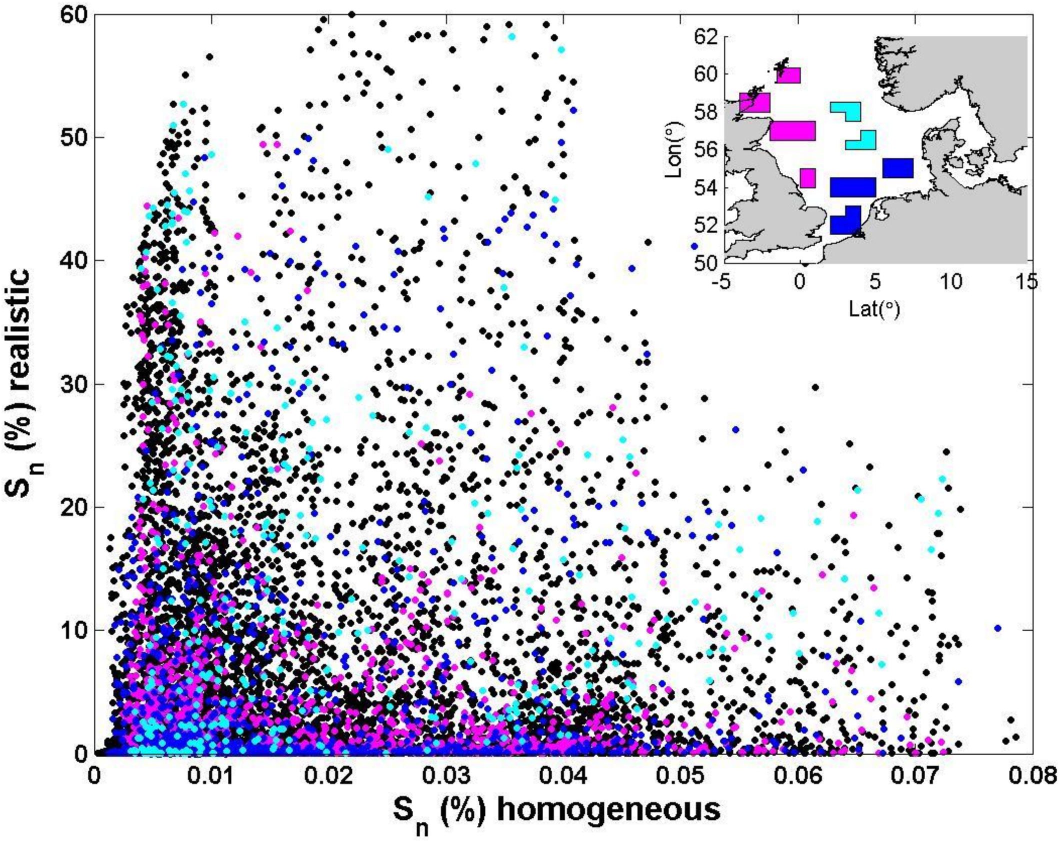
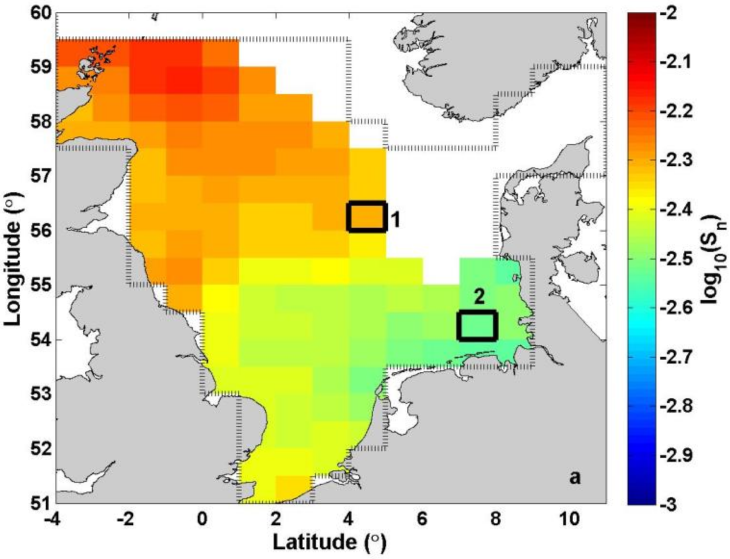


**Figure 7.4. Mean ELS survival $S_n$ (in %) obtained in the homogeneous simulation vs $S_n$ obtained in the realistic simulation. Black points show the mean survival in ICES rectangles outside the spawning areas. $S_n$ obtained within ICES rectangles overlapping with spawning areas (shown in the inset) are shown in colors.**



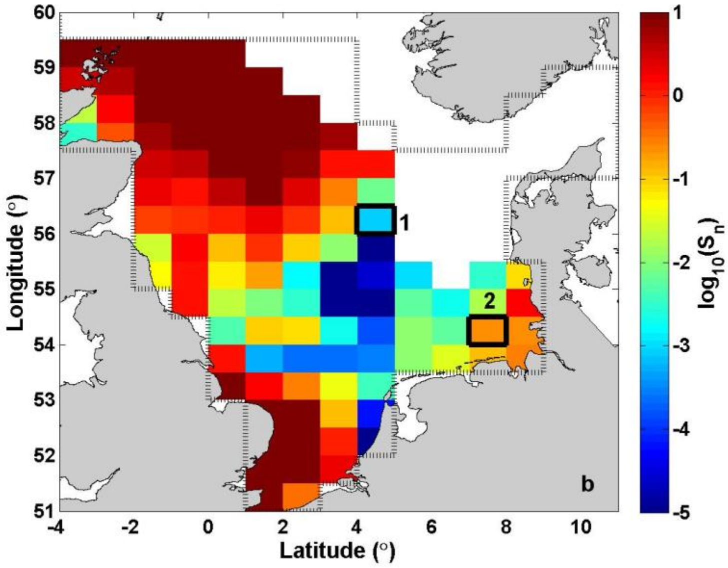


**Figure 7.5. Maps of the simulated survival of a cod cohort released on 20th of February 1992. Panel (a) depicts the log-transformed survival $S_n$ obtained in the homogeneous simulation, panel (b) – in the realistic simulations. Solid line bounds rectangles, discussed in text and referred in Figure 7.6 and 8.7. Dashed line bounds all ICES rectangles where super-individuals were released during the simulation. White areas within dashed bound are the ICES rectangles, for which $S_n$ could not be estimated due to the drift of super-individuals out of the model domain.**

An examination of the temperature and survival trajectories of an "average" super-individual ($S_r \approx S_n$) from each of the grid cells (SI1 and SI2 correspondingly, Figure 7.6) helps to illustrate why these contrasting patterns were observed between the predator scenarios (**Figure** 7.7). During the egg and early larval stage (until the age of 60 days), the survival of SI2 was higher than SI1 in the homogenous scenario (**Figure** 7.7, panel b) due to the colder temperatures (lower instantaneous mortality according to Eq. 7.12) experienced by SI1. After 60 days ambient temperatures experienced by SI2 were warmer than those of SI1 (**Figure** 7.7, panel a) and the survival of SI2 declined more rapidly than SI1 (**Figure** 7.7, panel b). This resulted in a lower ELS survival of SI2 in comparison with SI1 (**Figure** 7.7, panel b).

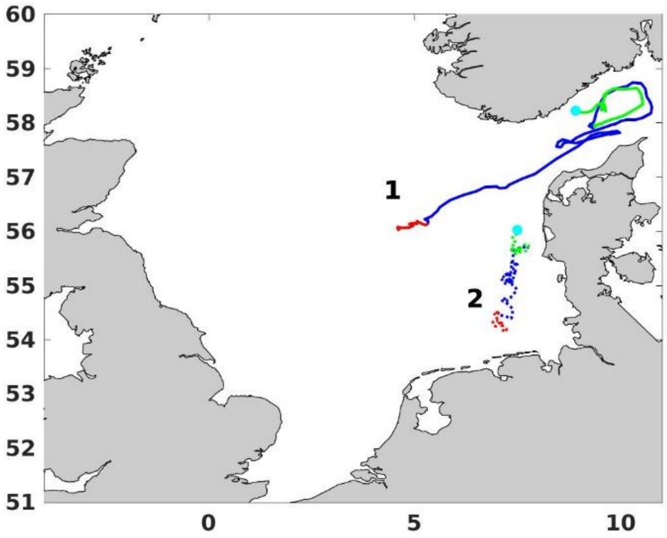


**Figure 7.6. Trajectories of two representative super-individuals SI1 (solid curves) and SI2 (dashed curves) released in the grid-cells 1 and 2 marked in Figure 7.5. Colors illustrate the developmental stages of the super-individuals (red – egg, blue - larval, green – pelagic juvenile, cyan – demersal juvenile)**

In the simulation with the realistic predation, both super-individuals experienced not only different temperatures, but also encountered fewer or greater amounts of predators along their drift trajectories (**Figure** 7.7c). Super-individual SI1 experienced stronger predation pressure during the egg and early larval stages (**Figure** 7.7c) which resulted in a rapid decline in survival as compared to SI2 (**Figure** 7.7d). During the juvenile stage (between the ages of 120 and 220 days) SI2 experienced higher predation pressure but this only marginally affected the total survival. In contrast to the homogenous predator simulation, by the end of the realistic simulation, SI1 had a higher survival than SI2. This example illustrates more clearly spatial differences in the modelled survival as well as differences between two scenarios.

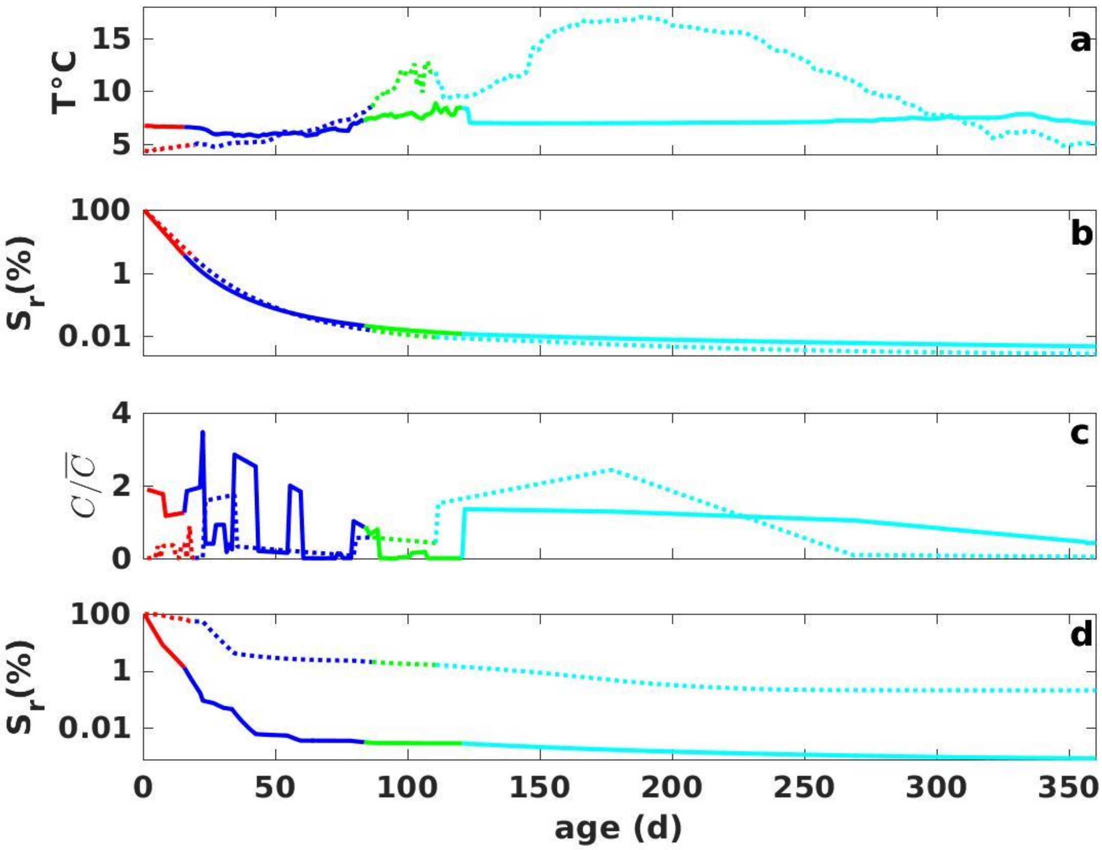


**Figure 7.7. Comparison of two representative super-individuals SI1 (solid line) and SI2 (dashed line) released in the grid-cells 1 and 2 (see Figure 7.5). Panel a: temperature the super-individuals experienced along their trajectories. Panel b: super-individual survival $S_r$ in the simulation with the homogeneous predator distributions. Panel c: predator consumption ratio $\frac{C}{\overline{C}}$ (Eq. 7.12) the super-individuals experienced in the simulation with the realistic predator distributions. Panel d: super-individual survival $S_r$ in the simulation with the realistic predator distributions. Trajectories of the super-individuals are shown in Figure 7.6.**

### *7.4.2 Sensitivity analyses*

The "hydrography" experiment resulted in the lowest inter-annual variability of cod ELS survival during all stages when compared to other experiments (Figure 7.8a). The weakest influence of hydrographical variability was predicted during the larval ($c_v = 3\%$; green box) and pelagic juvenile stages ($c_v = 2\%$; yellow box). As for the changes in predator biomasses and distributions, the relative importance of both factors varied among the developmental stages of cod. The influence of predator redistribution was stronger than the effect of the changes in predator biomasses during the larval stage (14% vs. 7%; Figure 7.8b and c, green boxes) and weaker during the demersal juvenile stage (12% vs. 19%; Figure 7.8b and c, cyan boxes). Similar responses to both factors were obtained during the egg and pelagic juvenile stages (Figure 7.8b and c, red and yellow boxes). The survival variability during the entire early-life period showed the strongest response in the "predation distribution" experiment ($c_v = 25\%$; Figure 7.8c, blue box) followed by the response to the changes in predator biomasses ($c_v = 13\%$; Figure 7.8b, blue box) and in hydrographic conditions ($c_v = 9\%$; Figure 7.8a, blue box).

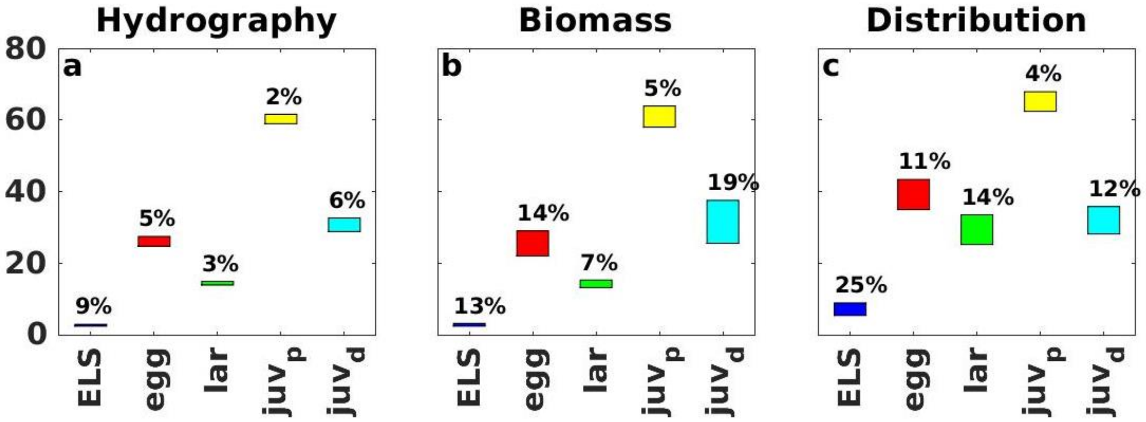


**Figure 7.8. Results of the sensitivity experiments "hydrography" (panel a), "predator biomass" (panel b) and "predator distribution" (panel c). Location of the boxes shows the mean survival during the early-life period (ELS; blue), as well as egg (egg; red), larval (lar; green), pelagic ($juv_p$; yellow) and demersal ($juv_d$; cian) juvenile stages. The width of the boxes depicts the standard deviation $\sigma_y$ of the survival estimates. The numbers are corresponding coefficients of variation $c_v$ (in %).**

### *7.4.3 Survival of cod ELS released in known spawning areas*

Survival of the cod cohorts simulated with the realistic predation varied substantially among the spawning areas (Figure 7.9). Three spawning areas (Dogger Bank (DB), German Bight (GB) and Flamborough (Fl) were associated with predominantly low cohort-specific survival $S_c$ (Figure 7.9 a, b and c) and relatively low mean survival over the simulated period ($\overline{S_{sa}}$ below 2.5 %). Intermediate mean survival ($\overline{S_{sa}}$ from 3.2 to 7.9%) was predicted for three spawning grounds in the central and northern North Sea (northeast of Scotland (NES), Forties (Fo) and Fisher Bank (SB); Figure 7.9 d, e and f). Cohorts spawned in these areas had predominantly low survival ($S_{sa}$ <10 %) but rare events of the relative high survival were also predicted. High mean survival ($\overline{S_{sa}}$ from 12.9 to 19.5%) was predicted for three spawning areas: Southern Bight (SB), east of Shetland (ES) and at Ling Bank (LB) (Figure 7.9 g, h and i). Although the survival averaged over the entire simulated period was high, a strong variability of the cohorts-specific survival between <1% and 50% was observed.

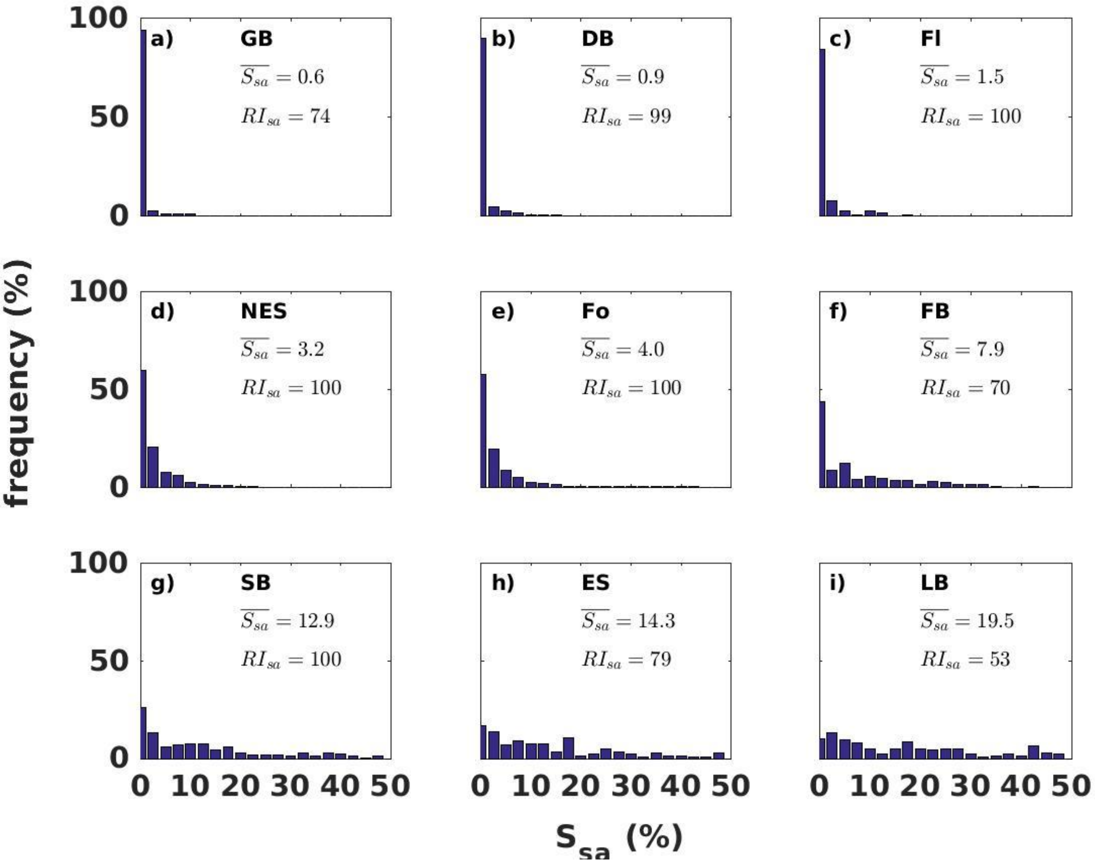


**Figure 7.9. Histograms of the cohort-specific survival $S_{sa}$ (in %) in the realistic simulation for cohorts released in known spawning areas of cod: German Bight (GB, panel a), Dogger Bank (DB, b), Flamborough (Fl, c), northeast of Scotland (NES, d), Forties (Fo, e), Fisher Bank (FB, f), Southern Bight (SB, g), East of Shetland (ES, h), Ling Bank (LB, i). Mean survival over the whole simulated period $\overline{S_{sa}}$ (in %) and mean retention index ($RI_{sa}$) are shown in each panel. Location of the spawning areas is shown in Figure 7.1.**

In 4 of the 9 spawning areas (ES, GB, FB, LB) the retention index $RI_{sa}$ lied between 53 and 79%, e.g. between 21 and 47% of the cohorts released in these spawning areas were advected out of the domain (Figure 7.9). In these areas, cohorts spawned early in season (January-February) tended to have a higher probability to leave the domain before settlement. An exception was LB, where cohorts spawned in April were partly advected out of the domain as well.

Our simulation with the realistic predation predicted inter-annual changes in ELS survival that were highly asynchronous among the spawning areas (Figure 7.10). The strongest variability between the years was predicted in SB, ES and LB areas, where annually mean survival $S_{sa\,y}$ fluctuated between 2 and 42 % (Figure 7.10 g, h and i).

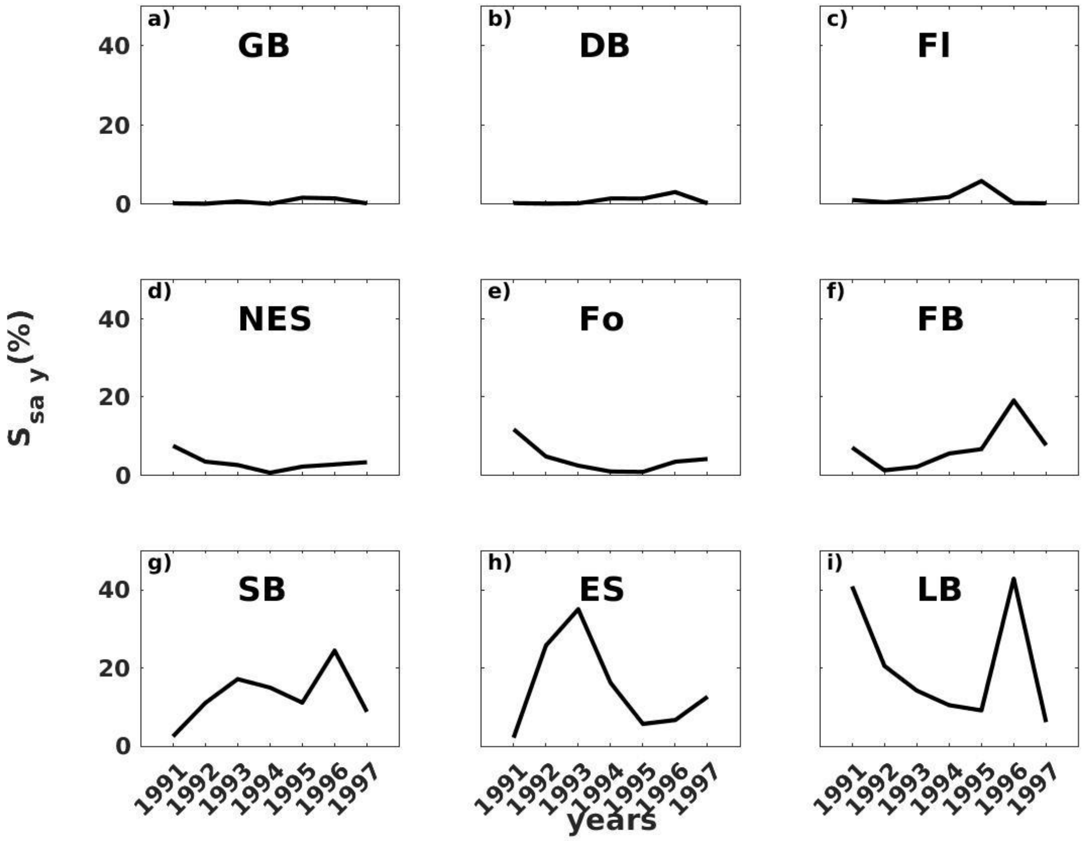


**Figure 7.10. Time-series of the annual mean survival $S_{sa\,y}$ (in %) in the realistic simulation in each spawning area: German Bight (GB, panel a), Dogger Bank (DB, b), Flamborough (Fl, c), northeast of Scotland (NES, d), Forties (Fo, e), Fisher Bank (FB, f), Southern Bight (SB, g), East of Shetland (ES, h), Ling Bank (LB, i). The location of the spawning areas is shown in Figure 7.1.**

## 7.5 Discussion

### *7.5.1 The importance of including realistic predation in cod ELS modelling*

Spatiotemporal „predator-prey" overlap has been widely discussed as an important control of the trophic interactions in marine and terrestrial ecosystems (*Kareira, 1990*; *Harrington et al., 1999*; *Edwards and Richardson, 2004*; *Grémillet et al., 2008*; *Hunsicker et al., 2013*). Within temperate marine ecosystems, the distribution of planktivorous and piscivorous predators (fishes, marine mammals and birds) is dynamic and varies both seasonally, due to migration to and from feeding and spawning areas, and annually due to environmental changes and fluctuations in the size of the population (*ICES, 1990*; *Corten and van de Kamp, 1992*; *Dalpadado et al., 2000*; *Engelhard et al., 2014*; *Montero-Serra et al.,* *2015*; *Pinnegar et al., 2016*). The importance of the spatial dynamics of planktivorous predators to zooplankton mortality has been demonstrated by introducing mobile predators within lower-trophic level models (*Travers and Shin, 2010*; *Maar et al., 2014*; *Huse and Fiksen, 2010*; *Utne et al., 2012*). However, spatially-variable predation has been seldom included in studies of fish early-life history (*Huse et al., 2004*; *Wiedmann, 2010*; *Petrik et al., 2014*; *Rose et al., 2015*). Our results for the North Sea cod emphasize the importance of including spatial dynamics of predators when attempting to estimates amounts of predation mortality experiences by marine fish early-life stages.

When comparing our predation scenarios (homogeneous vs realistic distribution), one of the most surprisingly results was two-order of magnitude higher survival of cod early life stages when realistic predator distributions were implemented (Figure 7.2). These results stem from the benefit of patchily distributed predators. In the homogeneous scenario, cod super-individuals encountered the same predator concentration everywhere, independent of their drift trajectory. Realistic patchy predator distributions (as observed in the survey data) is characterized by large areas of relative low predator concentration ("refuges") with patches of high predator concentration ("predator hot-spots"). The survival of cod super-individuals drifting passively through a patchy predator field depended not only on the total amount of predators in the domain but also on the probability of encountering either a "refuge" or a "hot-spot". This was demonstrated using an example of two super-individuals with contrasting survival between the homogeneous and realistic simulations (Figure 7.4). To demonstrate these effects at the population level, we calculated the ratio Q of days modelled super-individuals spend in "refuges" or in "hot-spots" (Eq. 7.16). Q was well above unity in each simulated year (Figure 7.3) indicating that super-individuals in the realistic simulation spent more time within ICES rectangles having predator concentration below that of the homogeneous simulation, i.e. in "refuges". This resulted in total survival being higher in the realistic simulation than in the simulation, in which predators were assumed to be evenly distributed.

The importance of a patchy distribution of marine organisms to the foraging success of predators and/or mortality rates experienced by prey has been previously discussed (*McGurk, 1986*; *Connell, 2000*; *Moore, 2001*; *Anderson, 2001*; *Temming et al., 2004*; *Temming et al., 2007*). *Temming et al. (2007)* reported an extremely high mortality of juvenile 0-group cod within local aggregations of whiting. An opposite effect, i.e. elevated larval survival in oligotrophic waters with relative low abundance of predators was assumed to underlie the observed spatial distribution of bluefin tuna (*Thunnus thynnus*) in the Mediterranean Sea (*Bakun, 2006*). Accordingly to our results, the North Sea cod benefits from the patchiness of its predators at the population level, although some cohorts encountering predator "hot-spots" might be swept away entirely.

Our model study clearly demonstrated that ignoring spatial dynamics of relevant predators can cause erroneous predictions of the survival of marine fish early-life stages as well as its year-to-year fluctuations. Compared to the homogenous distribution, realistic distribution of predators substantially altered not only the spatial pattern of the cod ELS survival (Figure 7.4) but also its inter-annual variability (Figure 7.2). Moreover, a strong correlation between the annual biomass of predators on the pelagic life stages and the survival of cod in the homogeneous simulation was absent in the simulation including observed (seasonal and annual) changes in the distribution of predators (Table 7.4). These results suggest that spatial dynamics of predators and redistribution of their “hot-spots” and “refuges” plays an important role in the regulation of cod ELS survival at the inter-annual scale. Our sensitivity experiments were designed to quantify the impact of predator redistributions on the year-to-year variability of cod survival and to compare it with the impacts of merely changes in the North Sea hydrography and predator biomasses.

We found that the modeled annual survival of cod ELS had the strongest response to the redistribution of the predators (25% of the mean survival; Figure 7.8c), followed by the response to the annual changes in predator biomasses (13%; Figure 7.8b). This was mainly caused by the high sensitivity of the larval survival to the redistribution of herring. The inter-annual variability of cod ELS survival was found to be least sensitive to the variability of hydrographical conditions (9%; Figure 7.8a), i.e. mutual effect of changes in the water circulation and temperature in the North Sea. This finding suggests that the spatial dynamics of predators has a more pronounced effect on the “predator-prey overlap” than changes in the dispersal pattern of the pelagic life stages of cod controlled by the strength of the cyclonic circulation in the North Sea. Therefore, our results underpin the importance of the spatial dynamics of planktivorous and piscivorous predators as an important factor regulating survival of cod through its first year of life. The importance of the spatiotemporal “predator-prey overlap” and its year-to-year-changes has been previously discussed for the North Sea cod recruitment by *Kempf et al. (2009)* and *Kempf et al. (2010)*. In both studies, the observed spatial overlap between demersal juvenile cod and its predators was incorporated into a 0-D trophic model and substantially improved its predictive skills. Our model results confirmed these previous findings, although this and previous studies (*Speirs et al., 2010*; *Akimova et al., 2016*) rather suggested that the predation on cod eggs and larvae is quantitatively more important for the prerecruit cod survival than the predation on its demersal juveniles. In the absence of long-term observational programs aiming at monitoring of cod egg and larval distribution, spatially-explicit modeling is a valuable tool to gain an insight into predation mortality of these stages and its spatiotemporal variability.

Although our model results provided an interesting insight into spatiotemporal interactions between cod ELS and its predators in the North Sea, we have to keep in mind that our approach of including the spatial dynamic of predators was very simplistic. We simulated predator dynamics based on the temporal interpolation of quarterly distributions of the main predators observed in field survey. Incorporation of a more realistic spatial dynamics of modelled predators by using spatial-distribution models or models of animal movements including foraging behavior and explicit seasonal migration (*Giske et al., 1998*; *Planque et al., 2011*; *Huse et al., 2004*; *Rose et al., 2010*) will allow to resolve prey-predation interactions at finer spatial and temporal scales than it is done in this study.

A word of caution is needed regarding the results of our sensitivity experiments. Since we aimed at the modelling of the entire first-year of life of the North Sea cod, our simulations were constrained to the period from 1991 to 1997, when quarterly data on predator distributions were available from the groundfish survey. This short period did not depict the whole range of observed stock biomass of some predators: the biomass of herring was rather close to its long-term mean during this period, biomasses of cod and grey gurnard were low in comparison to other period (Figure 7.11). As it has been shown for some fish stocks (*Swain and Sinclair, 1994*; *Rose and Leggett, 1991*; *Rose and Kulka, 1999*), the spatial distribution of a predator may relate to the size of its stock in agreement with the "basin hypothesis" of *MacCall (1990)*. Furthermore, climate-driven shifts in the distribution of both demersal (*Perry et al., 2005*) and pelagic (*Montero-Serra et al., 2015*) fishes have been documented in the North Sea and North Atlantic. Most prominent examples are the northward shifts of adult cod (*Hedger et al., 2004*; *Dulvy et al., 2008*) and herring (*Montero-Serra et al., 2015*), both are important predators on cod ELS. Such environment- and density-dependent changes of predator distributions may impact the overlap between cod early-life stages and their predators and therefore alter the results of the sensitivity experiments presented here.

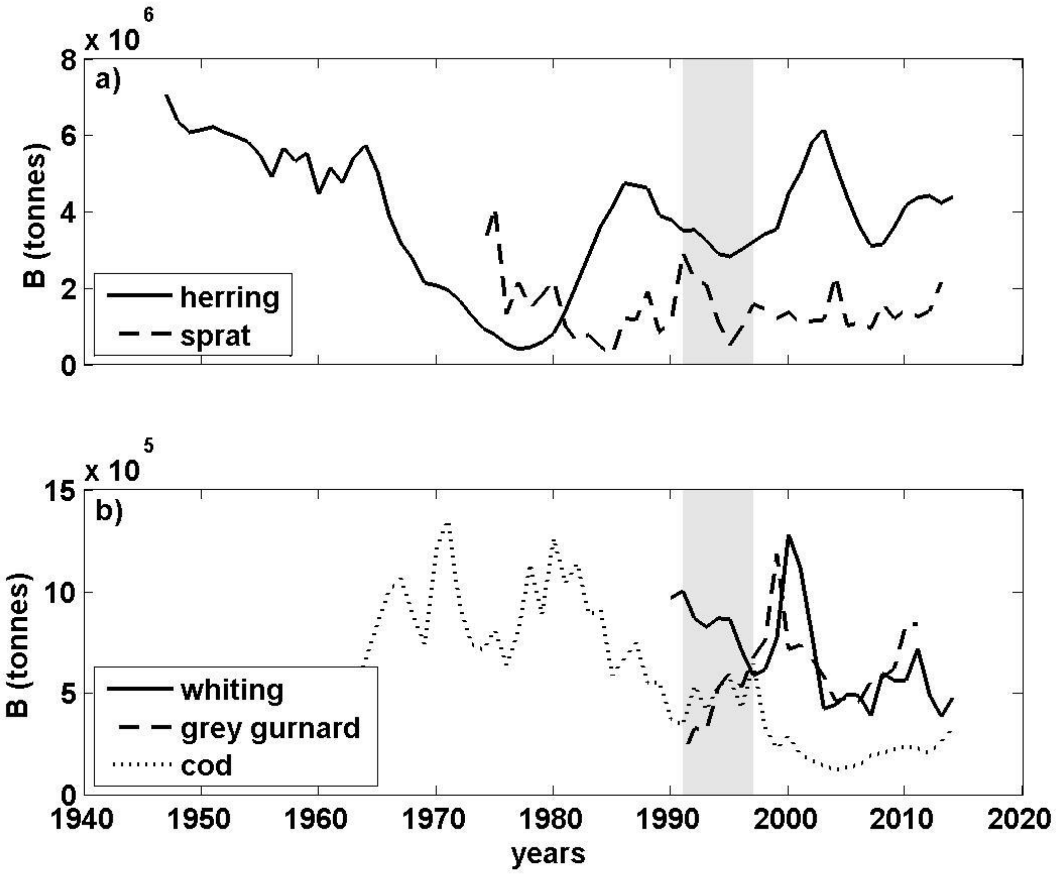


**Figure 7.11. Time-series of the total stock biomass (B, tonnes) of the main predators on the pelagic (panel a) and demersal (panel b) life-stages of cod in the North Sea. Following predators are shown: Atlantic herring *Clupea harengus* (panel a, solid line), European sprat *Sprattus sprattus* (panel b, dashed line), whiting *Merlangius merlangus* (panel b, solid line), grey gurnard *Eutrigla gurnardus* (panel b, dashed line), and Atlantic cod *Gadus morhua* (panel b, dotted line).**

### *7.5.2 Survival potential of cod spawning areas in the North Sea*

Our model with the realistic predator distributions predicted highly variable cohort-specific (Figure 7.9) and annual (Figure 7.10) survival of cod ELS released in the known spawning ground of cod in the North Sea (Figure 7.1, Table 7.3). When averaged over the simulated period, the lowest ELS survival was predicted in the spawning areas in the German Bight, at the Dogger Bank and west of the British coast (Figure 7.9a, b and c, Figure 7.1). This was mainly due to the high abundance of herring and sprat in the southern North Sea, where cod-individuals spawned in these areas spent their pelagic stages. In contract, highest mean survival was obtained for the super-individual spawned east of Scotland, at the Ling Bank or in the Southern Bight (Figure 7.9g, h and I, Figure 7.1). These areas are known to be less productive (*Daewel et al., 2011*) and planktivorous fishes are generally less abundant there, therefore cod eggs and larvae from these areas have better chances to survive. Substantial proportion of the cohorts released east of Scotland and at Ling bank were predicted to drift out of the North Sea before settlement. Such advective losses can be seen as another source of mortality, because these cohorts are lost for the North Sea cod population although they do not necessarily die.

This spatially-variable top-down control of cod survival demonstrated in this study, can be seen as a broadening of the "match-mismatch" concept of David Cushing (*Cushing, 1969*). This hypothesis, in its original formulation, considered the importance of temporal match between prey (zooplankton) and predator (fish larvae) for the survival of predator. Later this concept was extended to include temporal „match-mismatch" of fish ELS with their potential predators (*Bailey and Yen, 1983*; *Lafontaine and Leggett, 1988*; *Bailey and Houde, 1989*). However, fish ELS or other prey organisms can also benefit from the spatial mismatch with their predators, particularly when they are not the main food item of these predators (*van der Veer, 1985*; *Sih, 2005*; *Ciannelli et al., 2007*; *Kempf et al., 2013*). Our model study underpins the importance of both temporal and spatial "match-mismatch" between cod ELS and its predators for the survival of the young cod in the North Sea.

Our simulations with the realistic predator distributions suggested that each of known spawning areas contributed differently to the total survival and that this contribution varied from year to year (Figure 7.10). If we assume that spawning takes place only within these grounds and that spawning activity (number of spawned eggs) is evenly distributed among them, the total survival of cod offspring in the North Sea can be obtained by summing the survival over all spawning grounds. However, spawning activity of North Sea cod was shown to vary among the spawning areas and among the years within one spawning area (*Wright et al., 2003*; *Rindorf and Lewy, 2006*; *González-Irusta and Wright, 2016*) and the majority of cod spawning areas are occasional or recurrent (*González-Irusta and Wright, 2016*). Therefore, cod recruitment at the level of the entire stock is probably determined by the interplay between spatiotemporal fluctuations of the spawning activity and variable survival of fertilized eggs until the age of recruitment. Understanding of both processes, local spawning activity and offspring survival, is critical for the spatially-explicit fisheries regulations, establishment of fishery closures and marine protected areas (*CEFAS, 2001*; *Ciannelli et al., 2007*; *Kraus et al., 2009*; *Stelzenmüller et al., 2010*; *Hinrichsen et al., 2011*).

When considering the spatial pattern of cod ELS survival predicted by our model, one needs to keep in mind that only losses due to predation and advection out of the North Sea were considered. Starvation can be another important source of mortality of fish ELS and was not included here. Modelled larvae and juveniles had rates of growth close to the temperature-dependent ad-libitum growth (Eq. 7.1). A coupling of the growth physiology and foraging subroutines with a lower-trophic level model (*Daewel et al., 2011*; *Daewel et al., 2015*) suggested a profound spatial pattern of cod starvation, with the southern North Sea providing higher survival due to a higher concentration of suitable prey for young, exogenously feeding larvae compared to the northern North Sea. Visual comparison of the survival maps from *Daewel et al. (2011)* (their Figure 6) and the location of the spawning grounds used in our study (Figure 7.1) suggests that the four spawning areas in the southern North Sea (FI, SB, DB and GB) would provide better chances for surviving mortality than the spawning areas NES, Fo, LB and FB in the north. In contrast to those “bottom-up” results, our “top-down” simulations suggested that survival of cod ELS would be relatively low in the southern spawning areas and higher in the north where cod can take refuge from predators. In order to properly assess the potential benefit of cod using a specific spawning area, the cumulative effect of starvation, predation and retention over the early life stages needs to be considered. Moreover, the prey availability is expected to affects not only the probability of starvation but also the probability of growing at reduced (food-limited) growth rates (*Lough et al., 2005*; *Daewel et al., 2011*). This will likely modulate the magnitude of predation mortality due to a tight link between growth, size and vulnerability to predation of marine organisms (e.g. *Pepin and Shears, 1995*; *Meekan and Fortier, 1996*; *Houde, 1997*; *Hare and Cowen, 1997*; *Pepin et al., 2015*).

## 7.6 Acknowledgements

We thank Alexander Kempf for providing us the time-series the grey gurnard biomass from the stochastic multispecies model, Moritz Stäbler for providing some references for the discussion. We highly appreciate the contribution of all scientists, working on data collection and stock assessment within ICES and thank ICES Datacenter for providing technical support.

## 7.7 Appendix A: NS-IBTS data pre-processing

Data collected during NS-IBTS survey were incomplete for some years/quarters, i.e. not all ICES rectangles were sampled. To fill in such gaps, we used following procedure. If missing data were scarce (not more than 5 connected ICES rectangles), we used simple linear interpolation. If the data gaps were large (more than 5 connected ICES rectangles), we used a long-term mean proportion of CPUEs in these rectangles. It was the case in the 2nd quarters of 1996 and 1997, when ICES rectangles in the Southern Bight (south of 53.5°N) and in Skagerrak (east of 8.0°E) were not sampled. In the 4th quarter of 1997 only southern North Sea was sampled, therefore we used the long-term mean CPUE elsewhere.

In total, linear interpolated rectangles comprised 5.2% and replacements with the long-term means comprised 4.0% of all ICES rectangles in all quarters between 1991 and 1997.

## 7.8 Appendix B: Model stability

Our biophysical IBM used Lagrangian stochastic module to simulate drift of cod super-individuals. The results of such models are known to be sensitive to the number of super-individuals and under-sampling can lead to inaccurate or erroneous conclusions (*ICES, 2009*; *Petrik et al., 2014*). In our simulations, modelled trajectories of the super-individuals determined predator fields the super-individuals encounter and therefore the individual $S_r$ and mean $S_n$ survival associated with each ICES rectangle. Therefore, prior to scenarios simulations, we had to decide about the number of the super-individuals released in each ICES rectangle: this number should be big enough to produce statistically robust estimates of survival, but small enough to enable simulations in a reasonable computational time. One of the methods to decide about the minimum number of the super-individuals is to run simulations with various numbers of super-individuals and investigate how model output changes. Such performance or stability test is necessary to ensure that the output of the model is representative and does not depend on outliers, which might pollute the results.

To perform the stability test we started 10000 super-individuals in each ICES rectangle on an arbitrary spawning date (15th of February 1993). We calculated the cumulative mortality $M_{cum}$ (Eq. $7.13$) in each rectangle using all available super-individuals and assumed that this statistics represent ensemble mean of our model. Afterwards we subsampled the super-individuals with various subsampling size between 50 and 2500. For each subsampling size we drew 10 subsamples and calculated their mean and standard deviation. Figure 7.12 shows the standard deviation of the mean larval mortality estimated in an arbitrary ICES rectangle decreases with increasing sampling size. In our study we chose the threshold of the mortality accuracy of 5%, e.g. the minimum number of the super-individuals required for the statistical stability was defined as a sampling size at which the standard deviation of the subsamples fells within 5 % range of the ensemble mean. We also tested thresholds of 1% and 3 % of the mean mortality, but for these thresholds not all grid cells revealed convergence of the standard deviation. We found that at the sampling size of 1500 super-individuals the standard deviation converges with 5% threshold for all ICES rectangles tested.

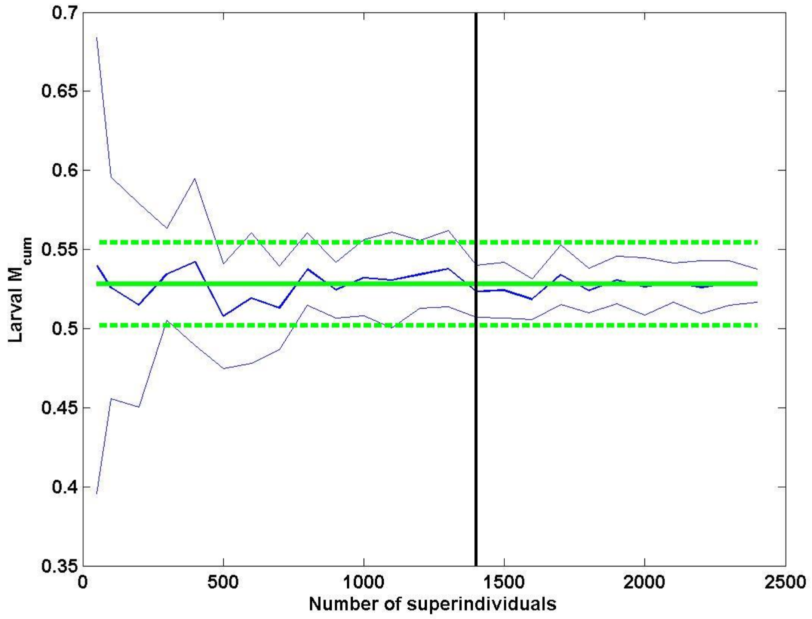


**Figure 7.12. Mean larval cumulative mortality $M_{cum}$ (blue thick line) and its standard deviation (blue thin lines) as functions of the number of sampled super-individuals. Green solid line shows ensemble mean calculated for all 10000 individuals. Green dashed lines show 5% deviation of the ensemble mean. Black vertical line shows minimal number of super-individuals required to ensure the robustness of the mortality estimates with 5 % accuracy.**

## 7.9 Appendix C: Consumption constraint

Eq. 7.12 is solvable in real number system for each time step ($\Delta t = 1$) only if the expression in logarithm is positive, i.e:

$$1 + \frac{C}{\bar{C}} \cdot (e^{-\bar{M}} - 1) > 0 \quad . \qquad 7.17$$

This condition put a constraint to the $\frac{C}{\bar{C}}$ ratio:

$$\frac{\mathrm{C}}{\bar{C}} < \frac{e^{\bar{M}}}{(e^{\bar{M}} - 1)}. \qquad 7.18$$

The solution of the inequality 7.18 is represented in Figure 7.13. The inequity 7.19 was violated in some ICES rectangles and super-individuals at the egg or early-larval stages. We assumed that super-individuals were consumed entirely within ICES rectangles they encounter if $\frac{\mathrm{C}}{\bar{C}}$ and $\bar{M}$ did not satisfy the inequality A2. For such super-individuals the cumulative mortality $M_{cum} = \infty$ and individual survival $S_r = 0$. This reflects an extreme strong consumption of prey in predator aggregations, as it was observed e.g. by *Temming et al. (2007)*.

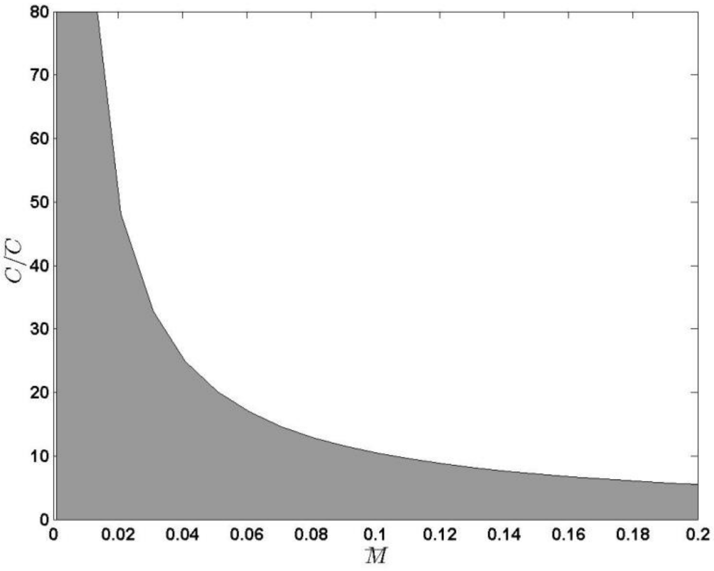


**Figure 7.13. Graphical representation of the inequality A2. Grey area depicts $\frac{c}{C}$ ratio that satisfy the inequality.**

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# 8 General discussion

Variable recruitment of marine fishes is one of the main problems of fishery science and a major source of uncertainty in management plans. Despite a substantial research effort during past decades, many aspects of fish recruitment are still not well understood. The intention of this thesis was to make another step toward a better understanding of the mechanisms responsible for the recruitment fluctuations of commercially important fish species in the North Sea. The findings of this thesis suggested a profound spatial variability of the biotic and abiotic processes affecting recruitment. In Chapter 5, regions of the North Sea were identified where environmental conditions seem to be more influential on year-to-year changes in stock recruitment, as well as other regions with little or no influence. These regions differed among fish species. For example, herring abundance was mainly influenced by temperature in the north-western North Sea, whereas recruitment of plaice was found to be strongly related to the temperature variations in the southern North Sea. In Chapter 7, predation mortality of cod ELSs was shown to vary substantially in space due to the inhomogeneous distribution of their predators. The importance of our understanding of the spatial heterogeneity of the North Sea ecosystem and its components including fish is discussed in Chapter 8.1 below based on the results of Chapters 4, 5, and 7.

One of the main goals of this thesis was to explore and evaluate mechanisms governing recruitment of North Sea cod. The results of Chapter 5 showed that cod recruitment is negatively correlated with water temperature in the north-western North Sea. These findings contributed to the discussion of possible mechanisms underlying the observed relationships between temperature and cod recruitment. In Chapter 6, water temperature was shown to influence both growth and mortality rates of cod ELSs. The mutual effect of the temperature-induced changes in these rates was found to affect the survival of cod through its early-life period. In Chapter 7, the importance of the year-to-year changes in temperature, biomass and the spatial distribution of predators for cod survival was studied. The findings of these three chapters concerning the mechanisms regulating recruitment success of North Sea cod are discussed in Chapter 8.2 in the context of previous studies.

Recruitment-related studies are mainly motivated by the need of improving current fishery management. Potential implications of the results obtained in Chapters 5 and 7 for cod fishery management and marine spatial planning in the North Sea are discussed in Chapter 8.3. Finally, Chapter 8.4 provides an outlook for further investigations needed to improve the reliability of the model-based estimates of cod recruitment in the North Sea.

## 8.1 Spatiotemporal variability of the North Sea ecosystem

This thesis aimed to study the spatiotemporal variability of the ecosystem processes driving recruitment variability of commercially important fish species in the North Sea. Data availability is generally the main limitation to explore spatially variable interactions between ecosystem components. Environmental data collected during previous decades in the North Sea are unevenly distributed both in space and in time and, therefore, mostly inappropriate to study the spatial and temporal variabilities simultaneously. To overcome this obstacle, a statistical method was applied to the available data to produced monthly maps of the North Sea hydrography suitable for ecological and fishery studies (AHOI; Chapter 4). The AHOI maps were further used in Chapter 5 to study spatially-resolved influence of temperature and salinity on the abundance and recruitment of nine commercial fish species. The AHOI maps were also applied elsewhere to investigate driving mechanisms of the North Sea salinity (*Núñez-Riboni and Akimova, 2017*), inter-annual variability in distribution of the pelagic fish species in the North Sea (*Keyl, 2017*) and the spatial structure of fish communities and life-history strategies (*Pecuchet et al., 2017; Frelat et al., 2017*). These studies demonstrated a usefulness of AHOI as a solid basis in the analyses of the environmental effects on the spatiotemporal variability of the North Sea ecosystem.

The spatially-explicit correlation analysis described in Chapter 5 allowed regions of the North Sea to be identified where environmental conditions were most strongly correlated to annual estimates of abundance and recruitment of the fish stocks. Different regions were identified for each fish species. The strongest correlation between cod recruitment and temperature was found in the north-western North Sea at depth of 60 m (Figure 5.2a), where the water temperature is mainly influenced by the inflow of the oceanic water from the North Atlantic (*Otto et al., 1990*; *Hjøllo et al., 2009*; *Mathis et al., 2015*). The strongest correlation between temperature and herring abundance was observed in the same region (Figure 5.3). In contrast, recruitment of the flatfish species, plaice and sole, revealed a negative correlation with temperature in the southern North Sea (Figure 5.4 and Figure 5.5), where temperature variability is mainly driven by local atmosphere-ocean interactions (*Berx and Hughes, 2009*; *Mathis et al., 2015*). These findings suggested that different physical processes drive the variability of the North Sea fishes. The identification of the areas of strongest environmental influence contributed to the discussion of the mechanism underlying the observed correlations, as it is discussed Chapters 5.6.1 - 5.6.4. Furthermore, the spatially-explicit analysis of Chapter 5 increased the explanatory power of the environmental covariates making them more reliable and suitable for the modeling of stock-recruitment relationships (SRR) for management purposes (*Planque et al., 2003*; *Subbey et al., 2014*).

Although the spatial heterogeneity of the North Sea hydrography is well documented (*Lee, 1980*; *Otto et al., 1990*; *Berx and Hughes, 2009*; *Hjøllo et al., 2009*; *Meyer et al., 2011*; *Mathis et al., 2015*; *Núñez-Riboni and Akimova, 2017*), relationships between abiotic and biotic variables have been often analyzed by averaging them over the entire North Sea (e.g. *Fox et al., 2000*; *Beaugrand et al., 2003*; *Planque and Frédou, 1999*; *Beaugrand, 2004*; *Reid et al., 2003*; *Teal et al., 2008*; *Gröger et al., 2010*). In the case of exploited fish species it was partially caused by the fact that most fish stocks in the North Sea are assessed and managed as single stocks without finer spatial management divisions (*ICES, 2012*; *ICES, 2015*). Analyses of the spatial variability of the ecosystem components have been mainly restricted to occasional observational campaigns (e.g. *Fox et al., 2008*; *Munk, 1993*; *Hoeffle et al., 2013*; *Van Ginderdeuren et al., 2013*).

The spatial heterogeneity of marine ecosystems has been previously suggested to be a major issue in our understanding of ecosystem responses to variable biotic and abiotic conditions (*Levin, 1992*; *Menge and Olson, 1990*; *Rose, 2000*; *Stenseth et al., 2004*; *Cury et al., 2008*). *Rose (2000)* showed that in some ecosystems their heterogeneity might lead to different or even opposite ecosystem responses to the consistent changes in environmental conditions. Spatial heterogeneity of the North Sea ecosystem is increasingly coming into the focus of the observational studies. It has been shown, for example, that zooplankton production and composition is substantially different in the northern and southern North Sea (e.g. *Planque and Fromentin, 1996*; *Beaugrand, 2004*; *Pitois and Fox, 2006*). Furthermore, demersal fish assemblages have been found to vary among regions of the North Sea with different hydrographic regimes (*Ehrich et al., 2009; Frelat et al., 2017*). There is an on-going discussion whether some of the North Sea fish stocks consist of several subpopulations with different temporal dynamics in their abundance and recruitment (*Wright et al., 2006*; *Heath et al., 2013*; *Neat et al., 2014*; *Payne, 2010*; *Dickey-Collas et al., 2010*). Moreover, *Kempf et al. (2013)*, *Hjermann et al. (2013)* demonstrated that species interactions in the North Sea also include pronounced spatial component.

Modeling is increasingly seen as a powerful tool to study spatially-variable processes and interactions in marine ecosystems (e.g. *Rose et al., 2010*; *Travers and Shin, 2010*; *Fulton et al., 2011*; *Peck et al., 2016*). Metapopuation or habitat models simulate an ecosystem as a set of populations or habitats connected by biomass fluxes, similar to box models in physical oceanography (*Levins, 1969*; *Kritzer and Sale, 2004*; *Heath et al., 2008*; *Huse et al., 2008*). Fully spatially-explicit models use fine two- or three dimensional grids and allow various ecosystem processes to be represented at various spatial scales. 3-D models have been successfully used to simulate oceanographic conditions (e.g. *Marsland et al., 2003*; *Pohlmann, 2006*; *Hjøllo et al., 2009*;) and dynamics of lower trophic levels in a wide variety of marine ecosystems (e.g. *Skogen et al., 1995*; *Wainwright et al., 2007*; *Kishi et al., 2007*). They are also increasingly applied to simulate the dynamics of upper-trophic levels, including fish (e.g., *Travers et al., 2007*; *Fulton et al., 2011*; *Politikos et al., 2015*; *Rose et al., 2015*). Biophysical, 3-D IBMs have been widely utilized to study early-life stages of marine organisms, their feeding success and dispersal (*Hinckley et al., 1996*; *Miller, 2007*; *Peck and Hufnagl, 2012*; *Hare, 2014*). To lesser extent, biophysical models have been used to study top-down controls of fish ELS mortality (*Huse et al., 2004*; *Petrik et al., 2014*; *Travers et al., 2010*; *Peck and Hufnagl, 2012*; *Rose et al., 2015*). The case study of the North Sea cod presented in Chapter 7 demonstrated the importance of considering spatial variability of predator-prey interactions when addressing predation mortality of fish ELSs in marine ecosystems.

## 8.2 Bottom-up and top-down drivers of cod recruitment in the North Sea

Abiotic (direct and indirect influence of temperature; Chapter 5) and biotic (predation; Chapters 6 and 7) drivers of the recruitment variability of North Sea cod were addressed in this thesis (Figure 8.1). In Chapter 5, known negative relationship between water temperature and cod recruitment (Figure 8.1A, *Planque and Frédou, 1999*; *Drinkwater, 2005*) were confirmed using the longest time-series of both variables so far. The relationship was found to be stable over the whole period of observations from 1963 to 2013. The novelty of this study was that the strongest significant correlation was identified in the north-western part of the North Sea (Figure 5.2), e.g., in the area known to be influenced by the inflow of the Atlantic Water (*Otto et al., 1990*; *Becker et al., 1997*; *Hjøllo et al., 2009*). The correlation with temperature in the other parts of the North Sea was also negative but weaker and insignificant.

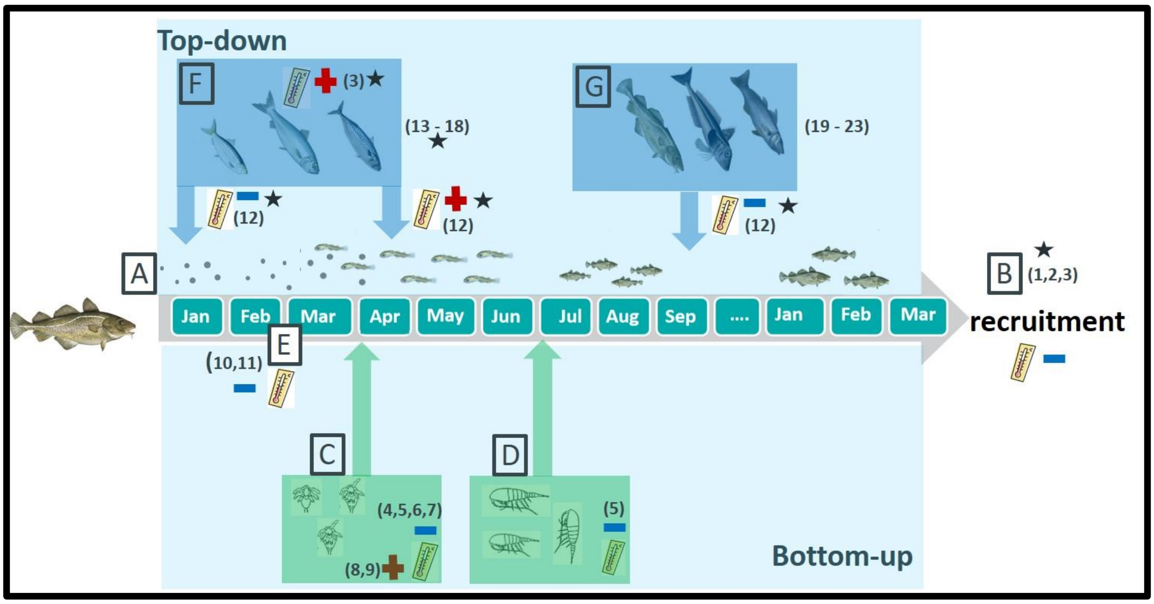

**Figure 8.1. The early-life period of North Sea cod between egg fertilization (A) and recruitment (B). Bottom-up (C, D, E) and top-down processes (F, G) regulating cod recruitment are shown. Positive ("+") and negative ("-") influence of temperature as suggested in previous studies and this thesis is shown. The contributions of this thesis are marked with black stars. Numbers refer to:**

**1 - *Planque and Frédou, 1999***
**2 - *Drinkwater, 2005***
**3 – *Chapter* 5 *of this thesis***
**4 - *Cushing, 1984***
**5 - *Beaugrand et al., 2003***
**6 - *Beaugrand and Kirby, 2010***
**7 - *Nicolas et al., 2014***
**8 - *Pitois and Fox, 2008***
**9 - *Kristiansen et al., 2011***
**10 - *Daewel et al., 2011***
**11 - *Daewel et al., 2015***
**12 – *Chapter* 6**
**13 - *Daan et al., 1985***
**14 - *Segers et al., 2007***
**15 - *Speirs et al., 2010***
**16 - *Minto and Worm, 2012***
**17 - *Hjermann et al., 2013***
**18 – *Chapter 7***
**19 - *Daan, 1989;***
**20 - *de Gee and Kikkert, 1993***
**21 - *Floeter and Temming, 2005***
**22 - *Temming et al., 2007***
**23 - *Kempf et al., 2009***

Starvation mortality and the temporal "match-mismatch" between cod larvae and their prey has been previously suggested to underlie the observed correlation between cod recruitment and water temperature in the North Sea (*Cushing, 1984*; *Beaugrand et al., 2003*; *Daewel et al., 2011*; *Kristiansen et al., 2011*; *Daewel et al., 2015*). Different aspects of the "match-mismatch" hypothesis have been considered. Cod larvae and pelagic juveniles are planktivorous with *Calanus/Pseudocalanus* species being a preferable prey items (*ICES, 1994*; *Rothschild, 1998*; *Munk, 1997*; *Robert et al., 2014*). *Beaugrand et al. (2003)* suggested two bottom-up controls of cod recruitment: i) changes in the zooplankton species composition affecting food availability for first-feeding larvae (Figure 8.1C), and ii) changes in the mean size of the calanoid copepods that affect prey quality of late larvae and young juveniles (Figure 8.1D). The observed changes in the zooplankton composition (*C. finmarchicus* vs. *C. helgolandicus*) were believed to alter zooplankton phenology and thereby affect the seasonal “match-mismatch” between cod first-feeding larvae and their prey (Figure 8.2, a and f). Both mechanisms suggested by *Beaugrand et al. (2003)* imply that increasing temperature diminishes survival of cod individuals through their early-life period either directly due to starvation or due to the poor nutrition, slow growth and higher mortality under the assumption of the size-dependent predation mortality. Combined effects of the temperature-induced zooplankton changes were found to explain almost 40% of the variability of cod recruitment in the North Sea (*Beaugrand and Kirby, 2010*).

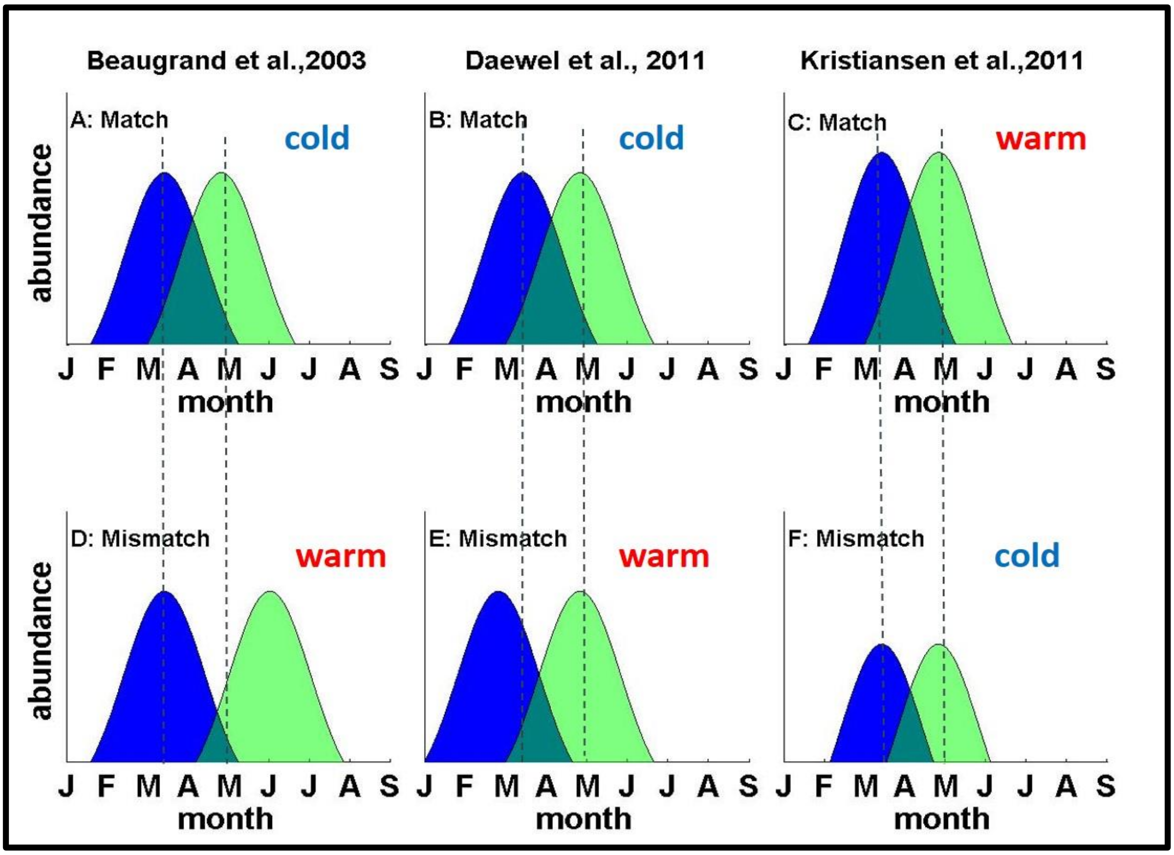

**Figure 8.2. Conceptual diagram of the temporal "match-mismatch" between cod exogenously feeding larvae (blue) and their suitable zooplankton prey (green). Three hypothesis are depicted: left panels show the match (panel A) and mismatch (panel D) according to *Beaugrand et al., 2003*; middle panels show match (panel B) and mismatch (panel E) situations according to *Daewel et al., 2011*; right panels show match (panel C) and mismatch (panel F) according to *Kristiansen et al., 2011***

*Pitois and Fox (2008)* questioned the first mechanism suggested by *Beaugrand et al. (2003)* as being a key factor determining recruitment variability of North Sea cod. They doubted the importance of *C. finmarchicus* as a preferred prey item of cod larvae and juveniles due to the spatial mismatch of young, exogenously feeding cod larvae with this zooplankton species in the North Sea. They pointed out that 1-group cod is predominantly caught in the southern North Sea (*Hjermann et al., 2013*; *Nicolas et al., 2014*). The simulations in this thesis showed that the majority of the juveniles that switch to benthic habitats in the southern North Sea spend their pelagic stages in this area as well. *C. finmarchicus* is a boreal zooplankton species and occupies mainly the cooler northern parts of the North Sea as it has been shown based on the data of the Continuous Plankton Recorder (CPR; *Planque* *and Fromentin, 1996*). However, *Nicolas et al. (2014)* suggested that *Calanus* ratio (the ratio between abundances of *C. finmarchicus* and *C. helgolandicus*) could be a proxy for changes in the abundance of other zooplankton species, which might affect the food quality of young cod larvae in the southern North Sea.

Moreover, *Pitois and Fox (2008)* showed by means of an empirical foraging model of larval cod that the observed concentrations of the suitable zooplankton prey were not a limiting factor for larval growth and survival, even during the periods when the abundance of key zooplankton species declined in the North Sea. Their model predicted elevated larval survival during warm years due to enhanced production of copepod nauplii observed in the North Sea. This finding of *Pitois and Fox (2008)* seems to contradict the first mechanism of *Beaugrand et al. (2003),* who suggested the negative effect of temperature on the survival of cod first-feeding larvae (Figure 8.1C). However, the model of *Pitois and Fox (2008)* was designed to study only the first 40 days of life of cod larvae. Therefore, the feeding success of cod late-larvae and juveniles as the second mechanism of *Beaugrand et al. (2003)* has not been tested in their study.

Additionally to the somewhat controversial indirect influence of temperature on cod recruitment, direct temperature effects have been considered as well. Model studies of *Daewel et al. (2011)* and *Daewel et al. (2015)* confirmed the importance of the "match-mismatch" dynamics for cod recruitment but suggested a different trigging mechanism. In these studies, the temporal "match-mismatch" between first-feeding larvae and their suitable prey was caused not by changing seasonality of the zooplankton production but by the temperature-dependent duration of the endogenously feeding life stages of cod (egg and yolk-sac larva, Figure 8.1E). Cod eggs and yolk-sac larvae were predicted to develop rapidly in warm years, leading to the temporal "mismatch" of cod first-feeding larvae with their suitable zooplankton prey (Figure 8.2, b and e). In contrast, cold water temperatures in late winter/spring were predicted to favour the temporal "match" of cod larvae with their prey and enhance larval survival. The inter-annual variability of cod survival was shown to be predominantly driven by the temperature changes in the southern North Sea, where zooplankton production was enough to support larval growth and survival (*Daewel et al., 2011*). Although the validity of the nearly constant seasonal peak of the zooplankton production is questionable (*Maar et al., 2014*; Dr. K Huebert, pers. comm.), the model study of *Daewel et al. (2015)* reproduced quite well the variability of cod recruitment observed from 1988 to 2000 (see their Figure 13).

Contradicting the findings of *Daewel et al. (2011)*, and *Daewel et al. (2015)*, the results of the model study of *Kristiansen et al. (2011)* suggested that survival of larval cod depends on the duration of the overlap („match") of cod larvae with their suitable prey and not on the timing of the peaks in the abundances of both organisms. *Kristiansen et al. (2011)* found that enhanced primary and secondary production during warm years cause a prolonged period of favourable feeding conditions, which, in turn, result in a better survival of cod larvae in four cod stocks in the North Atlantic, including the North Sea (Figure 8.2, c and f). These findings supported the results of *Pitois and Fox (2008)* about the positive influence of temperature on the larval survival of cod (Figure 8.1C), but contradicted the observed negative correlation between water temperature and cod recruitment in the North Sea (Figure 8.1A).

The findings in Chapter 5 of this thesis did not support the conclusions of *Daewel et al. (2011)* and *Daewel et al. (2015)* about the strong influence of local temperature conditions in the southern North Sea on cod recruitment. The correlation between cod recruitment and water temperature in the southern North Sea was weak (about -0.2) and insignificant. Similar results were obtained by *Nicolas et al. (2014)* by comparison water temperature and the observed abundance of demersal cod juveniles. To my understanding, the survival of cod larvae in the model study of *Daewel et al. (2011)* and *Daewel et al. (2015)* relied on the autochthonous (internal) zooplankton production in the North Sea, because their hydrodynamic and low-trophic level models did not include the variability of the Atlantic Water inflow (C. Schrum, pers. comm.). However, the Atlantic Water inflow has been previously shown to transport nutrients and zooplankton in the North Sea, thereby essentially affecting the dynamics of zooplankton organisms and their productivity (*Corten, 1999*; *Reid et al., 2003*; *Beaugrand, 2004*; *Papworth et al., 2016*). The results of Chapter 5 underpin the importance of the Atlantic Water inflow and its variability for cod recruitment in the North Sea. Whether the inflow affects cod recruitment by the bottom-up processes through altering zooplankton community and phenology as suggested by *Beaugrand et al. (2003)* or by influencing the strength of the top-down controls needs to be further investigated.

In my opinion, the role of starvation mortality as a factor controlling recruitment of North Sea cod remains somewhat unclear due to the inconsistencies of the previous findings described above. Our knowledge about prey preference of larval and juvenile cod is still quite sparse (*Olsen et al., 2011*; *Robert et al., 2014*) and seems to be insufficient to support or reject the link between larval starvation and recruitment. Additional field studies are required to assess the diet composition and prey selectivity of larval cod within different *in situ* feeding conditions and in different regions of the North Sea. Laboratory and model studies should be extended beyond the early-larval period (*Pitois and Fox, 2008*; *Daewel et al., 2011*; *Kristiansen et al., 2011*; *Huebert and Peck, 2014*) and include foraging and growth during the late-larvae and juvenile stages of cod. This additional research effort will hopefully help to reconcile the contrasting results obtained with respect to the importance of starvation mortality of cod ELSs in the North Sea.

Predation has been previously considered to be another important sources of mortality of cod ELSs based on direct observations (*Daan et al., 1985*; *de Gee and Kikkert, 1993*; *Greenstreet et al., 1997*; *Floeter and Temming, 2005*), time-series analyses (*Hjermann et al., 2013*; *Fauchald, 2010*; *Minto and Worm, 2012*) and multispecies models (*Floeter et al., 2005*; *Speirs et al., 2010*; *van Denderen and van Kooten, 2013*; *Kempf et al., 2013*). Predation of planktivorous fishes such as herring, sprat or mackerel on cod eggs and larvae (Figure 8.1F) has been discussed by *Daan et al. (1985)*, *Pope and Macer (1996)*, *Nash and Geffen (2012)*, *Minto and Worm (2012)* and *Segers et al. (2007)*, whereas piscivorous predators such as adult cod, whiting, grey gurnard and saithe have been reported to prey on demersal cod juveniles (Figure 8.1G, *Daan, 1989*; *Floeter and Temming, 2005*; *Temming et al., 2007*). The correlation analysis in Chapter 5 revealed a positive correlation between herring abundance and water temperature in the north-western North Sea, where the negative correlation between cod recruitment and temperature was observed (Figure 5.2, Figure 5.3 and Figure 8.1F). This led me to a suggestion that water temperature might indirectly affect cod recruitment not only through the bottom-up processes but also through the top-down controls by influencing, for example, the abundance of cod predators, their consumption rate or the extent of the spatiotemporal overlap between cod ELSs and their predators.

Numerous previous studies have revealed positive effects of increasing temperature on the consumption rate of marine fishes (e.g. *Jones, 1974*; *Andersen, 1999*; *Andersen, 2012*; *Temming et al., 2002*). Therefore, the first hypothesis to test was whether temperature-dependent changes in the consumption rate of cod predators could underlie the observed negative relationships between cod recruitment and water temperature. A lower predation mortality of cod ELSs during cold years was expected due to the dampened appetite and lower consumption rate of their main predators. The model study in Chapter 6 revealed that cod eggs experienced indeed a lower cumulative mortality in cold years (Figure 6.8a). However, this effect was weak, because the decrease of the instantaneous mortality rate due to the decreased consumption rate of herring and sprat were nearly canceled by the increased duration of the egg stage at low temperatures. The cumulative mortality of cod larvae decreased with increasing temperature due to the reduction in the duration of this stage, which had a stronger effect on the cumulative mortality than the increase of the instantaneous mortality due to increased consumption rate of herring (Figure 6.8b). The model predicted an opposite effect for juvenile cod. In juveniles, the cumulative mortality was found to increase if ambient temperature increased (Figure 6.8c). The cumulative mortality over the entire early-life period was found as the sum of the cumulative mortalities during egg, larval and juvenile stages and was predicted to decrease with increasing temperature, because larval mortality constituted the largest proportion of the total mortality of cod ELS in comparison with other developmental stages (Chapter 6.1). Therefore, the reduced instantaneous mortality at colder temperatures seems to be unlikely to cause enhanced cod recruitment during cold years.

A sensitivity experiment was conducted to compare the response of the modeled cumulative mortality to the temperature variations and to the fluctuations in the biomass of the main predators of cod ELSs in the North Sea. This experiment suggested that the observed year-to-year changes in the predator biomass has a stronger effect on the inter-annual variability of cod ELS mortality than the temperature-induced changes in predator consumption rates (Figure 8.3). These results were not included in the final version of Chapter 6 but they support the conclusion that the temperature-dependent predator consumption and its inter-annual variability is unlikely to significantly affect the recruitment success of North Sea cod.

In my opinion, a word of caution is needed to prevent an overinterpretation of the results obtained in Chapter 6. One has to keep in mind that the biophysical model used in this study did not include prey availability as an important factor controlling foraging and growth of exogenously feeding cod larvae and juveniles. Secondary production in the North Sea and, therefore, the prey availability for larval cod is likely to be temperature-dependent in the North Sea. As it is mentioned above, compositional changes in zooplankton community have been shown to associate with water temperature in the North Sea (*Beaugrand, 2004*). Furthermore, the seasonality of zooplankton population in the southern North Sea has been shown to associate with inter-annual differences in water temperature (*Greve et al., 2001*). Such indirect effects of temperature on the growth rates of exogenously feeding cod ELSs were not taken into account in the biophysical model in Chapter 6. Therefore, the conclusions of this study are valid for cod eggs but might alter if indirect temperature effects on the larval and juvenile growth are included.

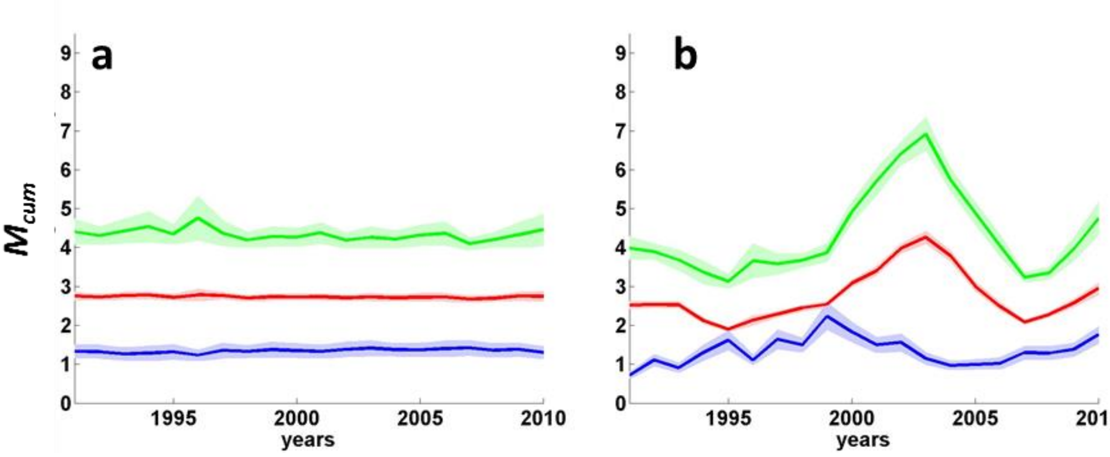

**Figure 8.3 Yearly-mean cumulative mortality ($M_{cum}$, no units) during the egg (red line), larval (greed line) and juvenile (blue line) stages of cod obtained in the sensitivity experiments with**

**variable temperature and constant predator biomasses (panel a) and with variable predator biomasses and fixed seasonal cycle of temperature (panel b). Shaded areas depict the standard deviation of the yearly mean mortality.**

The results of Chapter 6 allowed comparing, for the first time, the individual impacts of egg, larval and juvenile stages into cumulative predation mortality of cod during its first year of life. Larval mortality was estimated to constitute 53% of the total mortality (Chapter 6.1), followed by egg (36%) and juvenile mortalities (11%). The same ranking was predicted for the variability of predation mortality: larval mortality revealed the strongest inter-annual variability and juvenile mortality the weakest one. These results are in agreement with the study of *Speirs et al. (2010)*, who suggested the dominance of herring predation on cod eggs and larvae over the predation of grey gurnard on cod juveniles. The low fraction of the juvenile mortality in the estimated total mortality of cod ELSs and its weak inter-annual variability in comparison with other developmental stages do not support *Kempf et al. (2009)*, *Kempf et al. (2013),* who claimed the importance of the juvenile predation on the recruitment success of North Sea cod.

The model study in Chapter 7 demonstrated that predation mortality and survival of cod ELSs depend not only on the biomass of their main predators but also on predators' spatial distribution in the North Sea. These findings supported the previous studies of *Kareira (1990)*, *Huse et al. (2004), Ciannelli et al. (2007), Kempf et al. (2009)*, who suggested that the spatial "predator-prey" overlap is an important regulator of predation mortality of prey organisms in marine ecosystems. The spatial aspects of predation mortality of North Sea cod has been previously studied using observed distribution of cod juveniles and their predators (*Temming et al., 2007*; *Kempf et al., 2009*; *Kempf et al., 2010*; *Kempf et al., 2013*). *Temming et al. (2007)* demonstrated the importance of exceptionally small-scale, strong predation events of whiting on cod juveniles and, therefore, supported the idea of predation being the major source of pre-recruit mortality of cod in the North Sea. *Kempf et al. (2009)* claimed that cod recruitment results from the temperature-controlled interplay between bottom-up and top-down processes. They demonstrated that cod recruitment was strongly temperature-dependent if water temperature was below 9°C and recruitment was high. If water temperature was warmer than this threshold, no clear temperature effect on cod recruitment was observed and the "predator-prey" overlap was shown to drive the variability of cod recruitment. *Kempf et al. (2010)* reported a positive correlation between water temperature in the North Sea and the extent of the spatial overlap between juvenile cod and its demersal predators (grey gurnard, cod and whiting). To my knowledge, no observation-based assessment of the spatiotemporal overlap between the pelagic life stages of cod and their predators exists. In the absence of direct observations, modelling is the only available tool to gain insight in the spatial variability of predation mortality of cod eggs and larvae.

However, only 0-D models (*Floeter et al., 2005*; *Speirs et al., 2010*; *van Denderen and van Kooten, 2013*) or 3-D models with spatially-invariant predation (*Gallego, 2011*; *Kristiansen et al., 2011*) have been previously utilized to study predation mortality of cod ELSs in the North Sea. Both types of models did not take the spatial distribution of cod ELSs and their predators into account. The biophysical model in Chapter 7 represents, to my knowledge, the first attempt of analysing the spatial variability of predation on cod eggs and larvae and to assessing its impact on the inter-annual variability of cod ELS survival.

Although Chapter 7 provided an interesting insight into the potential dynamics of predation mortality of cod ELSs, one needs to be aware of assumptions applied in this biophysical model. For example, it is important to note that the model relied on the mean diets of cod predators obtained from the literature (*Greenstreet, 1996*; *Greenstreet et al., 1997*; *Floeter and Temming, 2005*; *Mackinson and Daskalov, 2007*). The proportion of cod ELSs in the diet of their predators was assumed to be constant in space and time. In the case of planktivorous fishes, however, it is still unclear whether they forage selectively (*Segers et al., 2007*; *Van Ginderdeuren et al., 2013*) or consume ichthyoplankton incidentally while foraging on zooplankton (*Pepin, 1987*; *Bailey and Houde, 1989*). The daily consumption of cod eggs and larvae could, therefore, depend on the presence of an alternative food source (mainly zooplankton), as it has been suggested for other fish species (*Brownell, 1985*; *Pepin, 1987*; *Pepin and Shears, 1995*). Given the observed spatial variability of the zooplankton biomass and production in the North Sea (*Fransz et al., 1991*; *Beaugrand, 2004*; *Pitois and Fox, 2006*), as well as including zooplankton in the diet of the modelled planktivorous predators might alter the estimates of cod survival obtained in Chapter 7. A throughout literature search will be required to parameterize such model and to test model sensitivity toward plausible parameter ranges.

The profound spatial variability of cod survival demonstrated in Chapter 7 and previous studies on starvation (*Daewel et al., 2011*; *Daewel et al., 2015*) underpins the importance of a better understanding of the spawning dynamics of North Sea cod. Data collected during egg surveys (*Daan, 1978*; *Heessen and Rijnsdorp, 1989*; *Brander, 1994*; Fox et al., 2008; *Munk et al., 2009*; Lelievre et al., 2014; *Höffle et al., 2017*) and NS-IBTS (*CEFAS, 2001*; *Wright et al., 2003*; Fox et al., 2008; *González-Irusta and Wright, 2016*) have been previously used to study spawning of cod in the North Sea. The spawning season has been shown to start in the beginning of January and last till late April – May (*Daan, 1978*, *Brander, 1994*, *ICES, 2005* and studies cited there). The seasonality of the spawning intensity of cod has been suggested to have a Gaussian form with a peak in mid-February in the southern North Sea and in April in the north (*Brander, 1994*). However, this conclusion was based on the observations obtained in different areas during different years and, therefore, the obtained seasonal signal could be "contaminated" with the inter-annual one. A later study of *Neuheimer and*

*MacKenzie (2014)* revealed no relations between the latitude and the mean calendar day of spawning of 21 cod stocks in the eastern Atlantic.

Atlantic cod is generally known to aggregate over specific grounds during the spawning period and return to these grounds over years (*Robichaud and Rose, 2001*; *Wright et al., 2006*; *Skjæraasen et al., 2011*). The previous studies on North Sea cod have suggested that cod spawning aggregations can be found almost over the entire North Sea, except its central parts (e.g. *Daan, 1978*; *Brander, 1994*; *CEFAS, 2001*; *Wright et al., 2003*; *Fox et al., 2008*). *González-Irusta and Wright (2016)* showed that most spawning grounds of cod are occasional and only few could be classified as recurrent. Unfortunately, the available observations are limited to resolve the spatial and temporal (seasonal and inter-annual) spawning dynamics simultaneously. To my knowledge, it is still unclear what triggers the spawning activity of North Sea cod and how its spawning period varies from year to year. *Brander (1994)* and *Morgan et al. (2013)* found no relation between water temperature and timing of spawning. *Brander (1994)* suggested a correspondence between the onset of primary production and the beginning of the spawning period of cod. However, later, *Lelièvre et al. (2014)* found no correlation between the observed egg density and the primary production in the southern North Sea. *Morgan et al. (2013)* demonstrated a clear impact of the age of spawners on the spawning time of cod in the North Sea and elsewhere in the North Atlantic. *Neuheimer and MacKenzie (2014)* revealed a significant correlation between the mean spawning date and fish thermal history of female cod for various cod populations in the North Atlantic. Whether the thermal history can be seen at the scale of the North Sea and how it might affect the duration of the spawning season remains unclear. *McQueen and Marshall (2017)* showed a significant trend toward earlier spawning over the last three decades but they did not analyse the inter-annual variability of the spawning period. In my opinion, our knowledge about cod spawning in the North Sea still have some critical knowledge gaps to be filled by an alternative statistical analysis of available data and/or by new directed observational programs.

The findings of this thesis together with the previous studies on cod early-life period demonstrated that the strength of processes potentially regulating year-class strength in cod such as prey availability, predator overlap and appetite, and reproduction of North Sea cod vary in space and time. Understanding of this variability is essential for understanding of the recruitment dynamics of cod. However, not only a better understanding of single processes (starvation, predation or parental effects) is required. The recruitment success of North Sea cod seems to be a result of a complex interplay of the bottom-up and top-down processes acting at different early-life stages. The interactions between different processes affecting growth and mortality rates of cod early-life stages need to be further investigated by combining field surveys, laboratory and field experiments and biophysical modelling.

## 8.3 Potential implications for fisheries management

Marine fishes exhibit strong inter-annual fluctuations in their abundance and productivity (*Rothschild, 1986*; *Fogarty et al., 1991*; *Vert-pre et al., 2013*). Lack of understanding of natural causes of these fluctuations has been named among the most important reasons for management failures in the past (*FAO, 2009*; *Beddington et al., 2007*). There have been numerous examples of severe depletion or even collapses of fish stocks caused by a combination of an intensive fishery and natural changes in stock productivity, which management plans failed to take into account (*Cook et al., 1997*; *Bailey, 2011*; *Mullon et al., 2005*). Therefore, a better understanding of the recruitment dynamics and improving its predictability has not only a theoretical but also an important applied aspect.

Some findings of this thesis can be used to improve the scientific advice needed by fisheries management and marine spatial planning. As it is shown in Chapter 5.6.5 using the example of North Sea cod, the obtained correlations between environmental parameters and fish recruitment can be used to improve “stock-recruitment” models utilized in fisheries management to predict the future dynamics of managed fish stocks in the North Sea (Figure 5.8; Table 5.3). Although the idea of the incorporation of environmental parameters into “stock-recruitment” models is not new (*Iles and Beverton, 1998*; *Olsen et al., 2011*; *Subbey et al., 2014*), a novel statistical method of choosing the best environmentally-modulated SRR model was proposed in Chapter 5.6.5.

To date, fisheries management is predominantly based on so called “single-species” approach, where the stock productivity is considered to be dependent only on the stock abundance (SRR, *Quinn and Collie, 2005*; *Beddington et al., 2007*). Other biotic and abiotic factors affecting recruitment dynamics are not taken into account in this concept. However, it has been shown that empirical SSRs often explain only a small fraction of the observed recruitment variance indicating that the productivity of marine fishes is partially driven by other factors than stock abundance (*Cushing, 1982*; *Vert-pre et al., 2013; Subbey et al., 2014*). It became increasingly obvious that the “single-species” approach is untenable and should be replaced by a new one, which consider multiple ecosystem components and users and the full array of interactions between them. A new approach called “ecosystem-based approach to fisheries management” (EBFM) has been suggested and formally adopted in 1990s (*FAO, 2009*). However, it is still extremely rare applied in fisheries management  and the majority of fish stocks worldwide are still managed using the “single-species” approach (*Möllmann et al., 2014*; *Skern-Mauritzen et al., 2016*; *Marshall et al., 2017*).

The recent stock assessment of North Sea cod includes at least some elements of the EBFM: Mortality estimates of the cod 1+ age groups depend on the biomass of cod’s main predators, such as larger cod, whiting, seals and porpoises (A. Kempf, pers. comm.). The recruitment of North Sea cod, however, is still predicted using SRR in its classical "single-species" formulation, despite multiple previous studies showing a substantial improvement of the SRR models when biotic and abiotic parameters are included (*Planque and Frédou, 1999; O'Brien et al., 2000; Olsen et al., 2011*). The findings of this thesis strongly support the notion that including water temperature as a covariate in the SRR models of North Sea cod would improve the robustness of SRR model estimates providing better science-based advice on stock dynamics to managers.

Several reasons for the lack of inclusion of ecosystem processes in assessment models has been previously discussed. The reasons include: i) "detectability" of the driving factors and the strength of the stock response (*Rose, 2000*), ii) non-stationary relationships between explanatory variables and stock dynamics (*Myers, 1998*; *Ottersen et al., 2013*), iii) an inability to predict environmental variables with a reasonable uncertainty at the time-scale relevant for management (*Planque et al., 2003*), and iv) the lack of understanding of the processes underlying observed correlations between environmental parameters and recruitment. A more precise identification of the region of the strongest temperature influence shown in Chapter 5 increased substantially the explanatory power of temperature on the variability of cod recruitment in comparison to the previous studies. Furthermore, it was demonstrated that the negative correlation between cod recruitment and water temperature is stable and equally strong over the entire period of observations (Figure 5.2), despite several regime shifts of the North Sea ecosystem in the last 50 years (*Reid et al., 2001* ; *Weijerman et al., 2005*; *Beaugrand et al., 2008*; *Beaugrand et al., 2014*). The suggestion about the influence of the North-Atlantic Inflow on the recruitment dynamics of North Sea cod (Chapter 5.5.1) opens also a possibility of a better predictability of the temperature changes in this region due to advective processes (*Becker and Pauly, 1996*; *Mathis et al., 2015*). To my opinion, all this makes North Sea cod an appropriate candidate for the implementation of an environmentally-modulated SRR model as one suggested in 5.6.5 in its fishery management. However, lack of understanding of the underlying process/processes remains a strong argument against including variable environmental conditions in the tactical management of cod. The identification of the mechanisms behind the observed relationship between water temperature and cod recruitment seems to be an intractable task given multiple biological processes potentially influencing cod recruitment (see Chapter 8.2). *Planque et al. (2003)*, however, argued that the inclusion of environmental factors in the tactical management of marine fishes may be beneficial even without a comprehensive understanding of the driving mechanisms. In such a case, a regular re-assessment of the management strategy would be required to account for the abrupt or gradual changes in the strength of the environmental influence on fish recruitment (*Skern-Mauritzen et al., 2016*).

As it is shown in Chapter 7, the survival of cod ELSs seemed to be determined, to a large extent, by the spatial dynamics of planktivorous and piscivorous predators and their yearly and seasonal redistribution in the North Sea. These results questioned the reliability of 0-D “multi-species” approaches (*Speirs et al., 2010*; *Floeter et al., 2005*; *Kempf et al., 2009*) and emphasized the need for greater biological realism in recruitment models. A new generation of management models have to be able to address the spatial variability of environmental processes and species interactions within a modelled ecosystem. The ongoing shift from 0-D “multi-species” to 3-D “ecosystem-based” approaches is a recognition of such requirements for the purposes of the EBFM (*Shin and Cury, 2001*; *Rose et al., 2010*; Fulton et al. 2011; *Collie et al., 2016*). However, there are still only few examples of such ecosystem models that include fully-resolved fish ELSs and simulate processes supporting their growth and survival (*Travers et al., 2010*; *Rose et al., 2015*; *Peck et al., 2016*). The results of Chapter 7 emphasized that “ecosystem-based” management models simulating the full life-cycle and recruitment dynamics of a modelled fish species need to consider spatially-explicit species interactions during fish early-life period.

The major objective of fisheries management is to control fishing mortality in order to maintain the biomass and productivity of commercially exploited fish stocks and prevent their overexploitation. There is a wide spectrum of controls and measures to regulate fishing mortality including regulation of the amount of fish caught, the size and the age of catches, and spatial and temporal controls on fishing (*FAO, 2009*). The later measure aims to protect fish species in vulnerable life stages and implies fishery closures in certain areas and seasons. Such closures are often implemented to protect spawning aggregations of commercially important fishes to enhance their productivity (*Murawski et al., 2000*; *Hu and Wroblewski, 2009*; *Clarke et al., 2015*; *Grüss et al., 2014*). The profound spatial variability of the survival of the cod ELSs in the North Sea predicted in Chapter 7 suggests that the effectiveness of a fishery closure depends not only on the spawning activity within a protected spawning ground but also on the probability of the produced offspring to survive the months ahead fertilization. According to the survival estimates obtained in this thesis (Figure 7.10), protecting females from fishing mortality when at spawning areas in the Southern Bight or east of Scotland may be more beneficial to enhance the year-class strength of cod than protecting females at spawning sites in the German Bight, Dogger Bank or Fisher Banks. In these latter areas cod eggs and larvae are more likely to be consumed by herring and sprat (Figure 7.1; Figure 7.10). These model results can be utilized to evaluate the potential benefit of the spawning area closures or marine protected areas (MPAs) for the recovery of North Sea cod. But prior to providing a scientific advice, the biophysical model needs to be further extended to include at least starvation as an important source of mortality of cod ELSs in the North Sea (*Beaugrand et al., 2003*; *Daewel et al., 2015*).

Although early-life stage IBMs have been successfully applied in fisheries science for several decades, they have been rarely directly used for the purposes of fishery management (*Hinrichsen et al., 2011*). To date, these models have been mainly utilized as exploratory tools aiming to advance understanding of how physical and biological factors may act alone or together to affect the growth and survival of fish ELSs. However, biophysical models have a great potential for application in the scientific advisory process informing marine fisheries management either as a stand-alone tools or embedded within more comprehensive fully coupled end-to-end models (*Miller, 2007*; *Fogarty and Botsford, 2007*; *ICES, 2009*; *Hinrichsen et al., 2011*). Numerous previous studies have demonstrated the weakness of the conventional "single–species" approach widely used in fisheries management (e.g. *Bax, 1998*; *FAO, 2009*; *Möllmann et al., 2014*). The results obtained in Chapter 7 support the importance of the multispecies consideration for recruitment forecasting but criticize 0D approaches for ignoring the spatial variability in the strength of species interactions. Fisheries management demands new quantitative tools that are able to combine bottom-up and top-down processes driving recruitment and to simulate their spatiotemporal variability. However, widespread use of 3D biophysical (and ecosystem) models in recruitment forecasting for fisheries management will probably stay limited until the performance and uncertainties of such models are better explored. Lack of appropriate data for model parameterization, calibration and validation is often one of the main limitations. Existing biophysical models can and should be used to identify major knowledge gaps and to support data collection required to improve model precision and predictive capabilities, as discussed below.

## 8.4 Outlook

Although a growing body of evidences exists about the spatial heterogeneity of the North Sea ecosystem and its components, we are seemingly still in the very beginning of collecting appropriate data and developing methods allowing to resolve processes at the relevant spatial and temporal scales and to integrate them over the entire ecosystem and a period of several decades. The results of this thesis emphasizes that a better understanding of how components of the North Sea ecosystem vary and interact in space is essential for understanding their temporal dynamics. Particularly, there is a need for further investigation of how spatially variable bottom-up and top-down controls regulate year-to-year fluctuations of fish recruitment.

"Predator-prey" interactions during the pre-recruitment period of life of marine fishes is increasingly seen as an important process regulating recruitment. These interactions are notoriously difficult to observe in the field, particularly when fish ELSs are involved. Fish eggs and larvae are extremely difficult to catch and identify (*Heath, 1992*). Ichthyoplankton are normally less abundant than other planktonic organisms such as zooplankton and are, therefore, challenging to observe using automated, non-invasive imaging systems. They are also very fragile and easily damaged in nets. Furthermore, fish ELSs, particularly fish larvae, are extremely problematic to detect in the stomach of their predators due to the rapid digestion and disintegration. Development of new techniques and analytical methods during the last decades substantially advanced our ability to catch and identify larval fish (e.g. *Houde, 2008*). However, regular observational programs are still technically and financially challenging. Therefore, field observations on the abundance of fish ELSs and field-based estimations of their predation mortality are extremely sparse. Even well studied marine ecosystem, such as the North Sea ecosystem, are acute undersampled with respect to fish ELSs and their predators. Therefore, "predator-prey" interactions during fish early-life stages are still poorly understood. Biophysical models, such one used in this thesis, can be utilized to identify parameters, regions and seasons, toward which model-based estimates of recruitment are most sensitive. This information can be used as additional help in identifying future research needs and designing observational programs and laboratory experiments focusing on studying these key parameters.

The majority of coupled biophysical models have been developed as explanatory tools to study processes that are difficult to observe at the appropriate temporal and spatial scales. Such models have substantially advanced our understanding of the drivers of the recruitment variability in many fish stocks (*Miller, 2007*; *Peck and Hufnagl, 2012*; *Hare, 2014*). However, we need to keep in mind that all models heavily rely on their parameterizations and, therefore, field or laboratory data underlying these parameterizations. In the absence of appropriate data, modelers are forced to make assumptions that might greatly affect the model dynamics. The uncertainty about parameters or processes included in a model propagates in the model and increase the uncertainty of the model predictions. Furthermore, observational and laboratory data is needed for the validation of existing biophysical models. Lack of appropriate data for model parameterization and validation is often the major obstacle of the model development. It strongly affects the reliability of a model, its confidence and the degree of trust from fisheries scientists and stakeholders.

Long-time series of stock assessment are valuable to identify trends in the stock abundance and recruitment variability, but their not spatially-resolved and provide only one data point per year. This data is definitely not enough to validate spatially-explicit mechanistic biophysical models. A regular larval survey exist for some fish species in the North Sea, as for example, the International Herring Larval Survey (*ICES, 2016*). For other species, such as cod or plaice, only sporadic observational campaigns have been conducted. Data collected during such campaigns are normally not included in international databanks and, therefore, difficult to achieve and proceed. To my understanding, ICES is currently making an effort to collect those data and make them available for the scientific community. Moreover, an ICES coordinated ichthyoplankton sampling of the entire North Sera have been conducted every five years since 2004 (*Taylor et al., 2007*; *Fox et al., 2008*). These data could be used to validate the early-life stage models of the North Sea fish species. I hope that new EBFM data obligations will broaden observational programs and provide additional opportunities to gather field data on fish ELSs.

The results obtained in Chapter 7 clearly demonstrated the need for further investigation of how spatially variable predation affects the survival of fish early-life stages in the North Sea. Planktivorous fishes such as herring, sprat, horse mackerel and mackerel consume a large amount of eggs and larvae of various fish species, for example, plaice, sole or herring (e.g. *Daan et al., 1985*; *Segers et al., 2007*; *Van Ginderdeuren et al., 2013*). Therefore, predation can strongly affect the recruitment dynamics of those fish species as well. The biophysical model used in this thesis can be applied to examine the role of predation mortality in fish species other than cod. Further improvements of the biophysical model developed in this thesis can be suggested:

1) Improving the representation of the predator fields in the model

Two methods can be suggested to simulate more realistically the dynamics of cod predators in the North Sea. The first approach is to develop a species distribution models (SDM) for each predator. Such SDMs predict the spatial distribution of the fish abundance in response to intrinsic, environmental, and anthropogenic factors. These models can be coupled to the biophysical model developed here and used to simulate the interactions between cod ELSs and their predators. To my knowledge, such SDMs do not exist for the fish species predating on cod ELSs in the North Sea, but some of them are currently in progress (I. Nunez-Riboni and M. Schaber, pers. comm.) An alternative method would be the development of a mechanistic model of animal movements (MAM) to simulate the spatial dynamics of cod predators at even finer spatial and temporal scales than it can be achieved using a SDM. This method is clearly more complicated and demands an advanced understanding of external and internal constrains on the individual fish movements (*Huse et al., 2004*; *Huse and Fiksen, 2010*). Coupling of the SDMs or MAMs with the biophysical model of cod ELSs will allow one to extend the model period beyond the period between 1991 and 1997, when quarterly data on the distribution of cod predators were available.

2) Studying possible effects of the spatially-variable abundance of alternative prey

The proportion of cod ELSs in the diet of their predators was assumed to be constant in the biophysical model used in this thesis. However, it has been previously suggested that the predation mortality of larval fish may depend on the presence of alternative prey of planktivorous predators (*Pepin, 1987*). Spatially- and temporally-variable zooplankton abundance obtained from a lower trophic level model can be used to examine the effects of zooplankton prey on the model-based estimates of the survival of cod ELSs and its spatiotemporal variability.

3) Incorporating realistic feeding and growth of cod ELSs

As it was mentioned above, several foraging IBMs of cod larvae exist (*Daewel et al., 2011; Kristiansen et al., 2011; Huebert and Peck, 2014*). Coupling of the model presented in this thesis with one of those models will allow one to quantify impacts of starvation and predation mortalities of cod ELSs. These two sources of mortality are notorious difficult to discern based on the field observations, therefore such model experiments could substantially contribute to the discussion about the role of both mortality processes in marine ecosystems. Furthermore, combining the bottom-up and top-down regulators in a single model will hopefully provide a new insight in the interplay between spatially-variable food-limited growth of cod ELS and size-dependent mortality.

I am looking forward to working on at least some of these improvements. I hope they will increase the confidence of model-derived estimates of cod ELSs survival and further advance our understanding of the bottom-up and top-down processes driving recruitment variability of North Sea cod.

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# 10 Declaration on oath

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 6th November 2017 Signature